The songs of the western European grasshoppers of the genus *Omocestus* in relation to their taxonomy (Orthoptera: Acrididae)

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Synopsis

The male calling songs of 11 western European and one Canary Island species of the Gomphocerine genus *Omocestus* are described and fully illustrated with oscillograms at three or four different speeds. The courtship song is also described for the six species in which such a song is known. The songs of six species (*panteli, bolivari, uhagonii, minutissimus, llorenteae* and *simonyi*) are described for the first time. For each species a full list is provided of references to any past published work on the songs, classified according to the kind of information given. Notes on recognition, using both morphology and song, are given for each species, and two identification keys are provided, one based mainly on morphology and the other on song. The value of the song as a taxonomic character is discussed.

Introduction

The Gomphocerinae, of which *Omocestus* is one of the better known Old World genera, include most of the common European grasshoppers of open grassland and moorland. They produce the most highly developed communicative sounds of all grasshoppers and are widely used in bio-acoustic, ecological and cytogenetic research. The subfamily includes about 150 European species, of which over 20 are pests in parts of their range, seven of them being regarded as major ones (Tsyplenkov, 1970).

Omocestus is a widespread Palaearctic genus, including some 40 species living in habitats ranging from lush lowland meadow to steppe, open woodland and high mountains. Twenty species have been recorded from western Europe, of which three, *rufipes, petraeus* and particularly *haemorrhoidalis*, become pests when they occur in sufficient numbers, causing damage to cereal grasses, hayfields, alfalfa and other cultivated plants in western and, especially, eastern Europe (Bei-Bienko & Mishchenko, 1951; Tsyplenkov, 1970).

The conspicuous songs of Gomphocerine grasshoppers have attracted attention for centuries,

but it is only since the pioneering work of Faber (1928) that they have been considered seriously as an aid to identification, and only during the past 30 years that their importance in taxonomic research, and particularly in resolving complexes of sibling species, has been fully recognized. This importance stems from the current belief that they provide the main mate recognition system in these insects and are thus able to maintain reproductive isolation in groups of sympatric species that would otherwise be able to interbreed freely. Perdeck (1957) established experimentally that this is true of the well-known sibling pair *Chorthippus brunneus* (Thunberg) and *C. biguttulus* (Linnaeus), and, although comparable studies on other groups of Gomphocerinae are still greatly needed, it seems likely that such studies would confirm that this function of the song is widespread in the subfamily.

Grasshopper songs can be quite easily recorded on tape and their rhythmic patterns, which provide the most useful taxonomic information, lend themselves well to oscillographic analysis. It is thus rather surprising that there has so far been no comprehensive account of these songs, presented group by group and illustrated with oscillograms. The main aim of the present paper, and of similar papers in preparation on other groups of Orthoptera, is to provide such an account, arranged systematically by group and fully illustrated with oscillograms at several different speeds. It is hoped that this form of presentation will make the information most useful in identification and taxonomy, as well as providing a basic reference work on the songs of these insects.

No information has previously been published on the songs of six of the 12 species included in this study (*panteli, bolivari, uhagonii, minutissimus, llorenteae* and *simonyi*) and no oscillograms have previously been published for a further two (*petraeus* and *raymondi*). For the species in which published information on the song is already available, references to the sources are given, classified according to the kind of information published. *O. simonyi*, known only from the Canary Islands, is not strictly within the scope of this paper but is included for convenience.

The song is still unknown in the following nine species of *Omocestus* recorded from western Europe: *antigai, burri, corsicus, femoralis, kaestneri, knipperi, lopadusae, navasi* and *uvarovi*. These species, which are all very local and often of doubtful status, are therefore excluded from this study.

Acknowledgements

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My thanks are also due to Dr N. D. Jago, who kindly provided me with tape recordings of the song of *O. viridulus* made by him in the French Alps; to Mr W. G. Tremewan, who was kind enough to collect live males of *O. panteli* for me in Teruel Province, Spain; and to Mr B. Alexander, who kindly brought me a live male of *O. simonyi* from Lanzarote, Canary Islands.

I am particularly grateful to my colleague Mr W. J. Reynolds, who made the studio recordings used in this study, helped me in reviewing the past literature on the songs, tested the identification key based on morphological characters and provided valuable comments at various stages in the preparation of the paper.

Finally I wish to thank my wife, who has given me invaluable help in all my field-work.

Abbreviations of depositories

BMNH	British Museum (Natural History), London
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin
ZI	Zoologiska Institution, Lunds Universitet, Lund

Methods

Recording and analysing the songs

All the field recordings of the songs used in this study were made while the insects were in full sunshine using a Uher 4000, 4200 or 4200IC tape recorder and AKG D202 or (recording 222/3 only) Shibaden microphone; the tape speed was always 19 cm/s. The subjects were approached stealthily so that the microphone could be held (or rested on the ground) about 10 cm from them without causing any disturbance.

The studio recordings were made in the BMNH Acoustic Laboratory using a Kudelski Nagra IV tape recorder and Sennheiser MKH405 microphone; the tape speed was 19 or 38 cm/s. In every case a bench lamp was used to provide light and radiant heat.

Further data are given in Tables 1 and 2 for the recordings used for the oscillograms reproduced in Figs 12–128. However, the song descriptions given for each species are in most cases based on many more recordings of numerous songs, all of which were analysed oscillographically. The oscillograms reproduced in the figures were chosen as being typical of the species concerned and, in some cases, showing the extent of intraspecific variation. Although I have given in Tables 1 and 2 the ambient air temperatures at the time of recording, it is really the body temperature of the singing insect that is important, and this is more dependent on radiant heat than on the air temperature; as the insects were always receiving radiant heat from the sun or a bench lamp, the conditions under which the recordings were made were more uniform than the different air temperatures might suggest.

All the oscillograms were made from recorded songs with a Mingograf 34T ink-jet recorder.

Song terminology

The bio-acoustic terms used are defined as follows.

Calling song. The song produced by an isolated male.

Courtship song. The special song produced by a male when close to a female.

Syllable. The sound produced by one complete up and down movement of the hind legs (Fig. 1).

Echeme. A first-order assemblage of syllables (Fig. 1).

Echeme-sequence. A first-order assemblage of echemes (Fig. 1).

Momentary breaks in the sound (of at least 1·25 ms) during the course of a syllable are referred to as 'gaps'.

Presentation

As the main purpose of this paper is to give information on songs, I have not included either a full synonymy or a formal morphological diagnosis in the account of each species. I have, however, listed references to all past descriptive accounts of the songs (of any significance), classified according to whether they include oscillograms (including sound-level tracings), diagrams (i.e. hand-drawn representations of the songs), frequency information, musical notation, or verbal description without any of these additions; any commercially available disc or cassette recordings of the songs are also listed. These references are not intended to be exhaustive – there are many brief statements about the songs, especially in the earlier literature, that do not warrant inclusion; my aim has been to list all sources that the reader might find useful to refer to for additional or confirmatory information on the songs. The only reference I have included to a work published before the present century is to Yersin's (1854) short but admirable account of the songs of 38 European species of Orthoptera (including two of *Omocestus*), in which he attempted, with some success, to represent them in terms of musical notation; in this largely forgotten work he demonstrated clearly for the first time the striking differences between the songs of the three closely similar species *Chorthippus brunneus* (Thunberg), *C. biguttulus* (Linnaeus) and *C. mollis* (Charpentier).

Notes are given for each species on recognition by both morphology and song, and these are

Table 1 Data for the field recordings of male songs of *Omocestus* used for oscillograms reproduced in this study. All these recordings were made from different males. Recordists' names are abbreviated as follows: NDJ = N. D. Jago; DRR = D. R. Ragge; WJR = W. J. Reynolds.

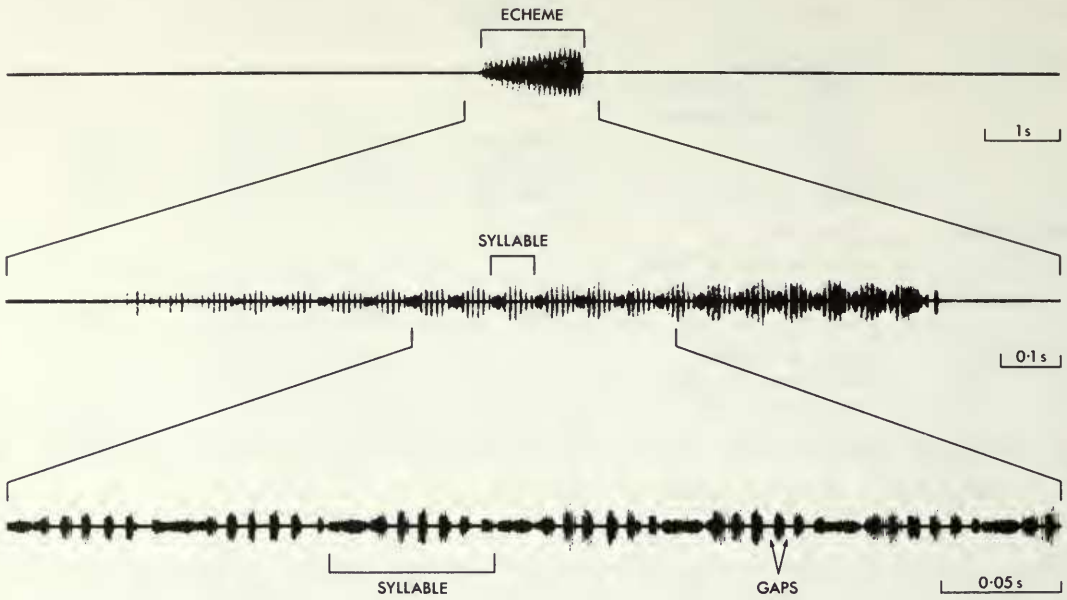
Species	Locality	Date recorded and collected	Recordist	Shade air temperature	Recording No.
viridulus	FRANCE: Alpes-Maritimes, near St Dalmas de Tende, Vallon de la Minière, 1830 m	26.viii.1977	NDJ	—	222/3
rufipes	AUSTRIA: Tyrol, near Kufstein, Kaisertal	13.viii.1973	DRR	24°C	98/3
	FRANCE: Hautes-Pyrénées, near Vielle-Aure, Neste de Couplan	20.ix.1976	WJR	14°C	183/2
haemorrhoidalis	FRANCE: Lozère, near Mende, Col de Montmirat	10.viii.1977	DRR	21°C	232/3
	FRANCE: Alpes-Maritimes, near St Martin Vésubie, Col St Martin, 1400 m	26.viii.1977	DRR	22°C	241/11
petraeus	FRANCE: Haute-Vienne, near St Yrieix-la-Perche	30.viii.1978	WJR	25°C	268/3
	FRANCE: Lozère, Causse Méjean, near Crosgarnon	31.vii.1982	DRR	20°C	482/5
raymondi	SPAIN: Huesca, 8 km E. of Ainsa.	3.ix.1978	WJR	31°C	270/8
	SPAIN: Madrid, Puerto de Galapagar, 800 m	17.vi.1984	DRR	30°C	531/3
	SPAIN: Granada, Sierra Nevada, near Capileira, 1500 m	22.vi.1984	DRR	24°C	532/4
panteli	SPAIN: Madrid, near Navacerrada, Valle de Barranca	27.vii.1983	DRR	22°C	503/5
	SPAIN: Granada, Sierra Nevada, Puerto de la Ragua, 2000 m	1.viii.1983	DRR	25°C	506/3
broelemanni	FRANCE: Pyrénées-Orientales, near Saillagouse, Val d'Eyne	15.ix.1978	WJR	23°C	276/3
bolivari	SPAIN: Granada, Sierra Nevada, Campos de Otero, 2300 m	31.vii.1983	DRR	21°C	505/4
	SPAIN: Granada, Sierra Nevada, Puerto de la Ragua, 2000 m	1.viii.1983	DRR	25°C	506/5
	Same locality	1.viii.1983	DRR	25°C	507/2

Table 1 – *cont.*

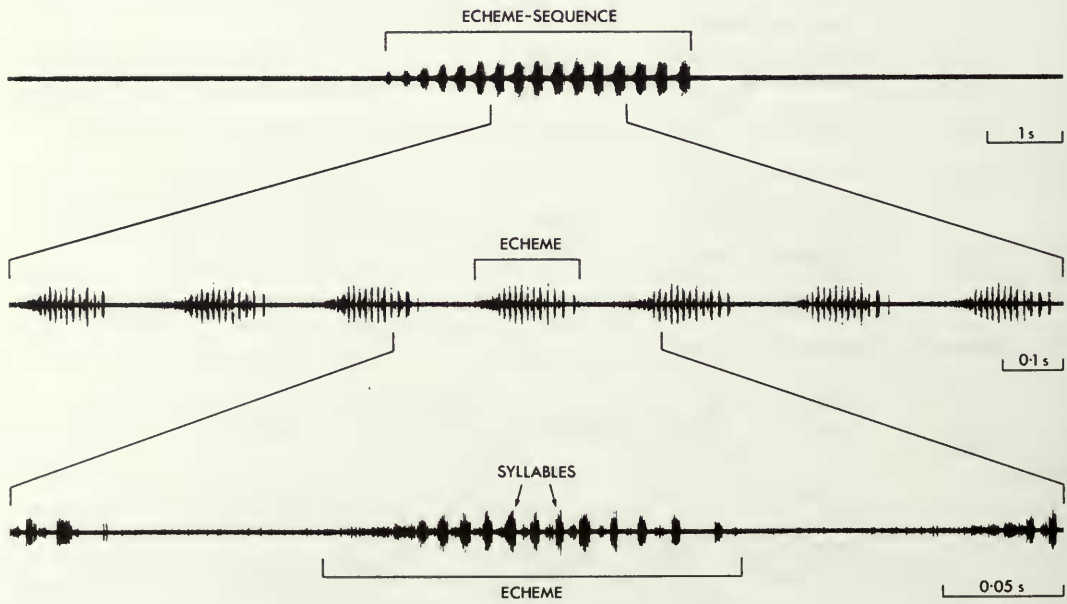
Species	Locality	Date recorded and collected	Recordist	Shade air temperature	Recording No.
uhagonii	SPAIN: Madrid, Sierra de Guadarrama, La Bola del Mundo, 2200 m	6.viii.1983	DRR	21°C	508/6
	Same locality	6.viii.1983	DRR	21°C	509/1
	Same locality	6.viii.1983	DRR	24°C	509/5
minutissimus	SPAIN: Madrid, Sierra de Guadarrama, Puerto de los Leones, 1500 m	5.viii.1983	DRR	23°C	508/3
llorenteae	SPAIN: Granada, Sierra Nevada, near Dornajo, 1900 m	30.vii.1983	DRR	27°C	504/6
	Same locality	30.vii.1983	DRR	27°C	505/1

Table 2 Data for the studio recordings of male songs of *Omocestus* used for oscillograms reproduced in this study. All these recordings were made from different males except for 310 and 312, which were made on different days from the same male of *panteli*. The recordist was W. J. Reynolds in every case.

Species	Locality	Date collected	Date recorded	Air temperature	Recording No.
viridulus	ENGLAND: Dorset, near Wareham, Morden Bog	18.vii.1976	21.vii.1976	29°C	168
	ENGLAND: Surrey, near Mytchett Lake	22.vii.1979	26.vii.1979	32°C	307/2
rufipes	ENGLAND: Kent, near Goudhurst, Bedgebury Forest	18.vii.1976	20.vii.1976	26°C	167/2
	ENGLAND: Hampshire, New Forest, Puttles Bridge	4.viii.1979	6.viii.1979	26°C	319
haemorrhoidalis	FRANCE: Pyrénées-Orientales, near Saillagouse, Val d'Eyne	22.ix.1976	29.ix.1976	26°C	177
panteli	SPAIN: Valencia, near Requena, 700 m	27.vii.1979	30.vii.1979	33°C	310
	Same locality	27.vii.1979	31.vii.1979	30°C	312
	Same locality	27.vii.1979	1.viii.1979	29°C	315
broelemanni	FRANCE: Pyrénées-Orientales, near Saillagouse, Val d'Eyne	15.ix.1978	19.ix.1978	25°C	266
simonyi	CANARY ISLANDS: Lanzarote, Teguise	12.ix.1982	15.ix.1982	28°C	562



Omocestus raymondi



Omocestus petraeus

Fig. 1 Oscillograms of the male calling songs of two species of *Omocestus*, showing the terminology used in this paper.

followed by a more detailed descriptive account of the calling song and, when known, courtship song. I have not attempted to describe any further kinds of sound produced by the males (e.g. 'rivalry song', 'copulation song') as these are not stereotypically patterned and seldom of diagnostic value. Neither have I considered it appropriate to describe the songs produced by females when in a sexually receptive state; these songs are seldom heard in the field and are in any case broadly similar in pattern to the calling songs of conspecific males.

The songs of each species are illustrated by oscillograms at three, or sometimes four, different speeds. As the scale lines indicate, the three speeds given for all species are (after reduction for printing) 10 mm/s, 80 mm/s and 320 mm/s, and the fourth speed included for the songs of three species (see below) is 1280 mm/s. In addition, oscillograms at 10 mm/s of typical male calling songs of all 12 species are shown together in Figs 12–23 so that the more obvious differences between them can be seen at a glance.

Grasshopper songs are normally produced by *both* hind legs being rubbed simultaneously against the fore wings, and oscillograms of such 'two-legged' songs show the sounds produced by the movement of one hind leg superimposed on those produced by the other. The two hind legs are not always well synchronized and in some species follow different patterns of movement, so that there is sometimes a degree of 'blurring' of the oscillogram. Moreover, in 'two-legged' oscillograms that are fast enough to show the impacts of individual stridulatory pegs, it is impossible to determine which peg-impacts are produced by one leg since these are mixed with those produced by the other. Although these points are not particularly relevant to the diagnostic value of the songs, I have thought it worth including for three species (*viridulus, rufipes* and *panteli*) oscillograms taken from the calling songs of males with only one hind leg. The difference between the 'one-legged' and 'two-legged' oscillograms is hardly apparent at the slower speeds, but becomes more obvious at 320 mm/s and clearer still at 1280 mm/s. The highest speed 'one-legged' oscillogram of *panteli* (Fig. 89) shows the individual peg-impacts with particular clarity.

The song as a taxonomic character

Recognition of the diagnostic value of the songs of Orthoptera may be said to have begun in the mid-nineteenth century, when Fischer (1849, 1850, 1853) published a number of song descriptions in primarily faunal or systematic works, and Yersin (1852, 1853 and especially 1854) produced a series of papers specifically on the songs and their value in identification. Yersin's work of 1854, in which he described the songs of 38 European species of Orthoptera, was particularly noteworthy in that it included the first attempt to illustrate the songs graphically, in the form of musical notation.

Little further progress was made in exploiting the songs in taxonomy until Faber's work of 1928, in which he gave, for the first time, an identification key to the German Orthoptera based on their songs. Many German studies on the songs of the European Orthoptera followed, notably by Faber (especially 1929, 1932 and 1936) and Jacobs (especially 1950), culminating in two major works published almost simultaneously (Faber, 1953; Jacobs, 1953). Most of this work was concerned with the detailed description of the songs and associated behaviour, and there was still no serious attempt to use the songs in taxonomic research.

Jacobs (1950, 1953) used simple diagrams against a time scale to illustrate the rhythmic patterns of the songs. Ragge (1965) introduced a more sophisticated kind of diagram, amounting to a simplified oscillogram, and diagrams of this kind have since been used by Holst (1970), Luquet (1978), Wallin (1979) and, in a slightly different form, by Duijm & Kruseman (1983) and Bellmann (1985). Identification keys based on the songs were provided, for restricted parts of Europe, by Luquet (the Mont Ventoux area of the French Alps, Acrididae only), Wallin (Sweden), Duijm & Kruseman (Benelux) and Bellmann (West Germany). All these studies are concerned with regional faunas and contain no taxonomic research, although Luquet gives much emphasis to the importance of the songs in taxonomy.

The first serious application of the songs of Orthoptera to their taxonomy was in work on the North American crickets (Gryllidae). Following the pioneering work of Fulton (1931, 1952),

Alexander (1957) and Alexander & Thomas (1959) reviewed the taxonomy of North American species of *Acheta* and *Nemobius*, and Walker (1962, 1963) carried out similar studies on Oecanthinae; in all these studies the songs played a crucial part in resolving the taxonomy of morphologically similar species. Similar work on other groups followed, some of it reviewed by Alexander (1962) and Walker (1964). In 1972 Alexander, Pace & Otte produced an account of the 'singing insects' of Michigan in which they gave keys based mainly on the songs for all the Ensifera.

More recent taxonomic studies on Orthoptera in which the songs have played a significant part include those of Bailey (1975, 1980) on African and Australian Copiphorine Tettigoniidae, Walker & Greenfield (1983) on Caribbean *Neoconocephalus* (Tettigoniidae), Otte & Alexander (1983) on Australian Gryllidae, Otte & Cade (1983 and later) on African Gryllidae, Heller (1984) on *Poecilimon* (Tettigoniidae) and Ragge & Reynolds (1984) on western European *Euchorthippus* (Acrididae).

As can be seen at a glance from Figs 12–23, the male calling songs of the western European species of *Omocestus* provide most useful taxonomic characters. Recorded songs, with appropriate oscillographic analyses, can be used to identify the species even if no specimens are available for morphological study (see the key on p. 224).

The calling songs of the 12 species embraced by the present study fall into two clearly different kinds: the rapid sequence of echemes produced by *petraeus, minutissimus* and *llorenteae*, and the single or widely separated echemes produced by the remaining species. As would be expected, the rapidly repeated echemes of *petraeus, minutissimus* and *llorenteae* are composed of very rapidly repeated syllables, almost always more than 80/s, whereas the syllable repetition rate of the remaining species is almost always less than 40/s. Within this trio of species *petraeus* stands a little apart from the other two in having even shorter and more rapidly repeated echemes, but the songs of *minutissimus* and *llorenteae* are broadly similar to each other in pattern, differing mainly in the duration of the echeme-sequence and the number of echemes of which it is composed.

Among the remaining species, *viridulus* and *rufipes* have much longer echemes than all the others; they are very similar to each other in both calling and courtship songs, differing mainly in the duration of the calling song echeme. The songs of all the other species consist of relatively short echemes distinguished from one another by duration, syllable repetition rate, and number and distribution of gaps. The song differences shown by the four brachypterous species *bolivari, uhagonii, minutissimus* and *llorenteae* are particularly useful for field identification; two or three of these species sometimes occur together in the same locality and are sufficiently similar in appearance to be quite easily confused with one another.

Extreme caution has to be used in drawing phylogenetic conclusions from resemblances or differences in grasshopper songs, since it is well known from studies on the *Chorthippus biguttulus* group that apparently closely related species, capable of producing vigorous and fertile hybrids, can have strikingly different songs. From the known songs of *Omocestus* I am inclined to make such inferences in only two cases of song resemblance. The first is the well-known pair *viridulus* and *rufipes*, in which the strong resemblance in both calling and courtship songs suggests that they are sister species. The second is the pair of brachypterous, montane species *minutissimus* and *llorenteae*, in which the close resemblance in calling song (as well as morphology) also suggests a comparatively recent common ancestry.

New lectotype designations

In the course of examining type-material I have taken the opportunity of designating lectotypes for the following species included in this study.

Gryllus rufipes Zetterstedt, 1821: 90.
Following Ander (1943: 10) I am regarding only two adult males from Zetterstedt's original material (in the ZI, Lund) as being eligible as syntypes, and I have selected and labelled one of these, bearing Zetterstedt's

ochre-yellow label (indicating Östergötland), as lectotype. I have labelled the other eligible adult male, which bears no colour-coded label, as a paralectotype.

Acridium petraeum Brisout, 1855: cxiv.
There is in the IRSNB, Brussels a long series of both sexes of this species, all labelled 'Lardy', the type-locality. These specimens are also labelled as being from the collection of de Selys Longchamps, who had earlier acquired Brisout's collection, and it seems almost certain that they include at least part of Brisout's type-series. I have selected and labelled a male bearing the handwritten label 'Lardy près de Paris' as lectotype. As there are many other specimens of this and various other species of *Omocestus* (and other genera) in the de Selys Longchamps Collection labelled 'Lardy', I have not attempted to determine which of these are also likely to belong to Brisout's type-series and so have labelled no specimens as paralectotypes.

Stenobothrus Brölemanni Azam, 1906: 128.
Dr M. Donskoff of the MNHN, Paris has kindly sent me the male from Azam's type-series that seems most eligible as a lectotype and I have so-labelled it.

Omocestus Bolivari Chopard, 1939: 172.
The type-series of this species (in the MNHN, Paris) consists of one male and one female, and I have selected and labelled the male as lectotype. The altitude given in the original description, '2000 m. environ', clashes with the '3000 m' given on the locality label, which I think is more likely to be accurate. I have labelled the female as a paralectotype.

Gomphocerus (Stenobothrus) Uhagonii Bolívar, 1876: 324.
Dr J. J. Presa of the Universidad de Murcia very kindly delivered to me by hand a male syntype of this species (from the MNCN, Madrid) labelled as being from Navarredonda, one of the type-localities, and I have labelled it as lectotype.

OMOCESTUS Bolívar

Omocestus Bolívar, 1878: 427 [as subgenus of *Gomphocerus* Thunberg]; Burr, 1904: 320 [raised to genus]. Type-species: *Gryllus Locusta viridulus* Linnaeus, by subsequent designation (Kirby, 1910: 172).
Dirshius Harz, 1975: 710 [as subgenus of *Omocestus* Bolívar]. Type-species: *Gryllus haemorrhoidalis* Charpentier, by original designation. **Syn. n.**

Diagnosis. ♂♀. Head of typical Gomphocerine shape, foveolae well developed. Antennae not clubbed. Pronotal lateral carinae varying from sharply incurved to almost straight. Brachypterous to macropterous. Fore wings without bulge on anterior margin of precostal area; medial area not conspicuously widened (except in *O. uvarovi* Zanon, whose generic assignment is uncertain). Hind wings varying from transparent to strongly smoky. Ovipositor varying in length, normally without lateral teeth but sometimes showing tendency towards their development (e.g. *O. broelemanni*). Tympanal aperture slit-like.

Discussion. *Omocestus* can be defined only on negative characters: it lacks the precostal bulge of *Chorthippus* Fieber, the toothed ovipositor of *Stenobothrus* Fischer, and the clubbed antennae of *Gomphocerus* Thunberg, *Gomphocerippus* Roberts and *Myrmeleotettix* Bolívar. Like several other genera in the large and rather intractable subfamily Gomphocerinae, it is no more than a group of convenience and is very unlikely to be holophyletic. Harz (1975) attempted to split it into two subgenera on the basis of the degree of curvature of the pronotal lateral carinae, but the species show every gradation between sharply incurved and almost straight carinae, and it is thus impossible to draw a clear dividing line between two subgroups.

Jago (1971) treated *Omocestus* as a subgenus of *Stenobothrus*, thus reverting to the status accorded to it by Bolívar (1897) and Yakobson & Bianki (1902). Jago's study was based entirely on males, however, and so did not take into account the toothed ovipositor as the main diagnostic character of *Stenobothrus* s. str. I prefer to follow Harz (1975) and other recent workers on the European fauna in regarding this character as sufficient for a generic distinction. Jago also regarded Kirby's designation of *viridulus* as the type-species of *Omocestus* as invalid on the grounds that, at the time of the original description of the genus, this species was listed by Bolívar (1878: 460) under *Chorthippus* rather than *Omocestus*. However, on p. 427 of Bolívar's work, where *Omocestus* is first established and diagnosed, *viridulus* is clearly included in it; the heading *'Chorthippus'* in the list on p. 460 has clearly been inadvertently misplaced, appearing above *rufipes* instead of in its correct position above *pullus*. I am therefore accepting Kirby's type-species designation as valid.

The male callings songs show a wide range of patterns in *Omocestus*, varying from the prolonged single

echemes of *viridulus* and *rufipes* to the rapid sequence of short echemes of *petraeus*. This is not in itself an indication of polyphyly, however, as some complexes of sibling grasshopper species that are capable of interbreeding (e.g. the *Chorthippus biguttulus* group) show equally striking differences in male calling song.

DISTRIBUTION. All Europe, the larger Mediterranean islands, North Africa and temperate Asia as far as China.

INCLUDED SPECIES. *O. alluaudi* Uvarov, *O. antigai* (Bolívar), *O. aymonissabaudiae* Salfi, *O. bolivari* Chopard, *O. broelemanni* (Azam), *O. burri* Uvarov, *O. caucasicus* Tarbinskii, *O. corsicus* Chopard, *O. cuonaensis* Yin, *O. demokidovi* Ramme, *O. enitor* Uvarov, *O. femoralis* Bolívar, *O. haemorrhoidalis* (Charpentier), *O. heymonsi* (Ramme), *O. hingstoni* Uvarov, *O. kaestneri* (Harz), *O. knipperi* Harz, *O. lecerfi* Chopard, *O. lepineyi* Chopard, *O. llorenteae* Pascual, *O. lopadusae* La Greca, *O. lucasii* (Brisout), *O. minutissimus* (Bolívar), *O. minutus* (Brullé), *O. megaoculus* Yin, *O. motuoensis* Yin, *O. nanus* Uvarov, *O. navasi* Bolívar, *O. nyalamus* Xia, *O. panteli* (Bolívar), *O. petraeus* (Brisout), *O. raymondi* (Yersin), *O. rufipes* (Zetterstedt), *O. simonyi* (Krauss), *O. tibetanus* Uvarov, *O. tzendsureni* Günther, *O. uhagonii* (Bolívar), *O. uvarovi* Zanon, *O. viridulus* (Linnaeus), *O. znojkoi* Mishchenko.

Keys to the principal western European species of *Omocestus*

The only western European species not included in these keys are very local forms, usually of doubtful status, in which the song is so far unknown.

Two keys are provided here, one based on morphological characters but with notes on song differences added where appropriate, and one based entirely on the male calling songs. Some of the species are very difficult to separate morphologically and, in the absence of song information, some specimens may not be correctly identified using the morphological key. Reference should in any case always be made to the notes given on recognition in the accounts of each species.

Key based primarily on morphological characters

This key is for sexually mature adults, either freshly collected or showing good colour preservation. *O. simonyi*, which is known only from the Canary Islands, is not included.

1 Rather brachypterous, fore wings less than 3 times length of pronotum 2
– Fully winged, fore wings more than 3 times length of pronotum 10

2 Larger: length of hind femur more than 9·2 mm in ♂, more than 11·0 mm in ♀. (Eastern Pyrenees and Catalonia) ..... ***broelemanni*** (p. 236)
– Smaller: length of hind femur less than 9·2 mm in ♂, less than 11·0 mm in ♀. (Not known from Pyrenees) 3

3 Fore wings not or hardly projecting beyond hind wings (when flexed); medial area with large dark spots 4
– Fore wings projecting well beyond hind wings (when flexed); medial area without spots 5

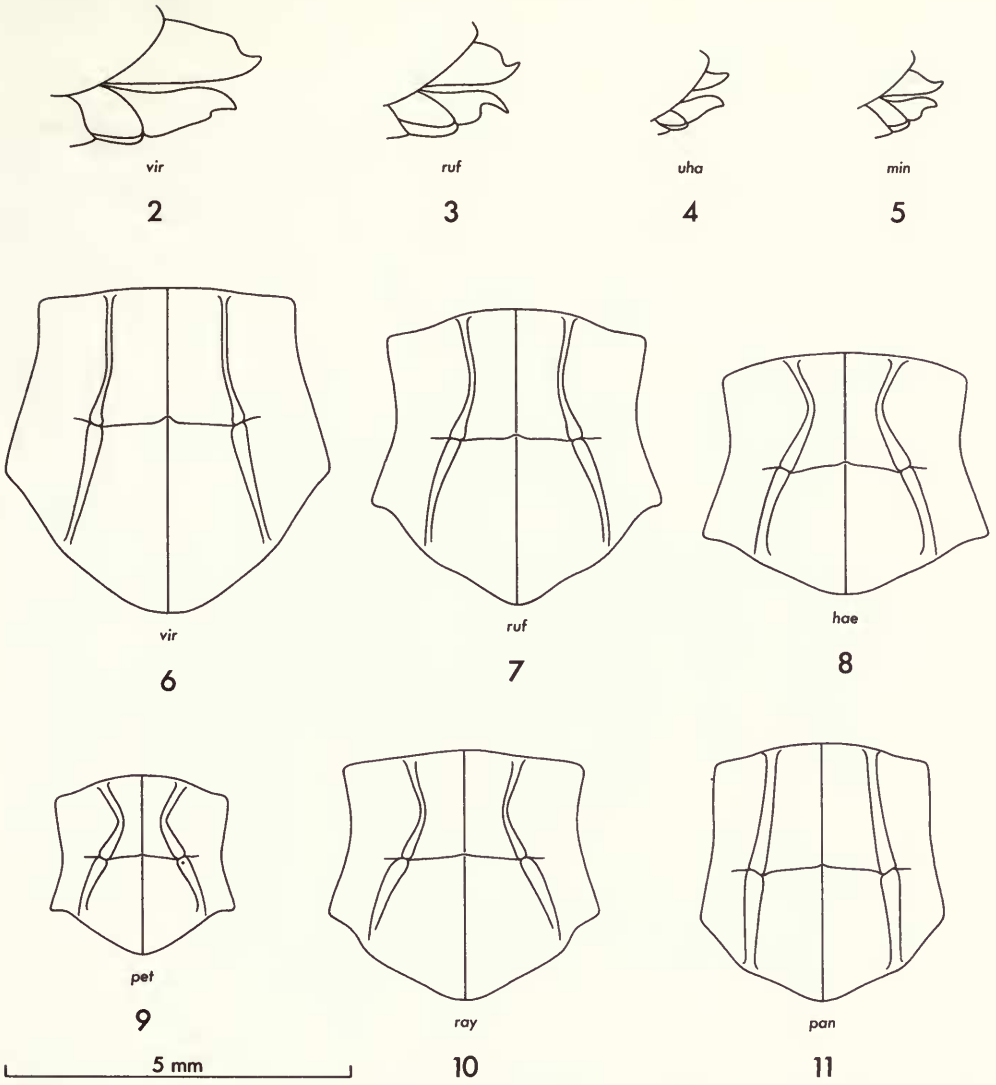
4 Fore wings more than 2·5 times length of pronotum in ♂, more than 2·1 times in ♀ ***llorenteae*** (p. 243)
– Fore wings less than 2·5 times length of pronotum in ♂, less than 2·1 times in ♀ ***minutissimus*** (p. 243)

5 Male 6
– Female 8

6 Cerci laterally compressed towards tip ..... ***uhagonii*** (p. 237)
– Cerci simply conical, not laterally compressed towards tip 7

7 Hind wings reaching less than halfway along fore wings (when flexed). Length of pronotum usually more than 2·5 mm. (Song a single echeme, as in Fig. 19) ..... ***bolivari*** (p. 237)
– Hind wings reaching more than halfway along fore wings (when flexed). Length of pronotum usually less than 2·5 mm. (Song a sequence of echemes, as in Fig. 21) ..... ***minutissimus*** (p. 243)

8 Fore wings less than 1·3 times length of pronotum ..... ***bolivari*** (p. 237)
– Fore wings more than 1·4 times length of pronotum 9



Figs 2–11 Ovipositors and pronota of species of *Omocestus*. 2–5. Lateral view of the ovipositor of (2) *O. viridulus*, (3) *O. rufipes*, (4) *O. uhagonii*, (5) *O. minutissimus*. 6–11. Dorsal view of the pronotum of (6) *O. viridulus*, (7) *O. rufipes*, (8) *O. haemorrhoidalis*, (9) *O. petraeus*, (10) *O. raymondi*, (11) *O. panteli*.

9 Ovipositor shaped as in Fig. 5, lower valves with strongly sigmoid ventral profile ***minutissimus*** (p. 243)

– Ovipositor shaped as in Fig. 4, lower valves with weakly sigmoid ventral profile ..... ***uhagonii*** (p. 237)

10 Pronotal lateral carinae straight or almost so in prozona (Fig. 11). (Iberian Peninsula) ***panteli*** (p. 236)

– Pronotal lateral carinae distinctly incurved or angled in prozona (not as in Fig. 11) 11

11 Fore wings falling well short of hind knees, their length less than 7·4 mm in ♂, less than 8·0 mm in ♀. (Mountains in S. Spain) ..... ***llorenteae*** (p. 243)

– Fore wings usually reaching at least to hind knees, their length more than 7·4 mm in ♂, more than 8·0 mm in ♀ 12

12 Hind wings completely transparent (except sometimes for part of the subcostal area). Pronotal lateral carinae as in Fig. 9. (Song a rapid sequence of echemes, as in Fig. 15) ..... ***petraeus*** (p. 233)

– Hind wings at least slightly smoky towards tip. Pronotal lateral carinae as in Figs 6, 7, 8 or 10. (Song a single echeme, repeated after an interval of at least several seconds) 13

13 Male 14
– Female 17

14 Abdomen with no orange or red colouring. (Song echeme lasting more than 12 s).. ***viridulus*** (p. 226)
– Abdomen with at least some orange or red colouring. (Song echeme lasting less than 12 s)..... 15

15 Abdomen with at least the distal 5 sternites coloured red or orange-red. Pronotal lateral carinae gently incurved in prozona, as in Fig. 7. (Song echeme lasting more than 4 s) ***rufipes*** (p. 227)
– Abdomen without reddish colouring on sternites or with such colouring restricted to the distal 3 or 4 sternites. Pronotal lateral carinae more strongly incurved in prozona, as in Figs 8 or 10. (Song echeme lasting less than 4 s) 16

16 Fore wings reaching well beyond hind knees, more than 4 times length of pronotum. (Song echeme lasting less than 2 s) ..... ***raymondi*** (p. 233)
– Fore wings not or hardly reaching hind knees, less than 4 times length of pronotum. (Song echeme lasting more than 2 s) ..... ***haemorrhoidalis*** (p. 227)

17 Ovipositor long, as in Fig. 2. Sides of body often green (but sometimes brown or reddish) ***viridulus*** (p. 226)
– Ovipositor shorter, similar in length to Fig. 3. Sides of body never green 18

18 Abdomen with at least the more distal sternites coloured red or orange-red. Pronotal lateral carinae gently incurved in prozona, as in Fig. 7..... ***rufipes*** (p. 227)
– Abdominal sternites with no reddish colouring. Pronotal lateral carinae more strongly incurved in prozona, as in Figs 8 or 10..... 19

19 Fore wings reaching beyond hind knees, more than 4 times length of pronotum ... ***raymondi*** (p. 233)
– Fore wings not or hardly reaching beyond hind knees, less than 4 times length of pronotum ***haemorrhoidalis*** (p. 227)

Key based on song characters (see especially Figs 12–23)

This key is based on the calling songs produced by isolated males in warm, sunny conditions. As far as couplet 5 the song differences can be easily detected by the human ear assisted by the second hand (or digital count) of a watch. From couplet 6 onwards some of the differences require oscillographic analysis, or at least the ability to play back the recorded song at a slower tape speed.

See p. 00 for definitions of the terms 'echeme', 'syllable' and 'gap'.

1 Song a series of echemes in rapid succession (at least 1/s) 2
– Song a single echeme or a series of echemes separated by intervals of at least 3 s 4

2 Echemes repeated at the rate of at least 3/s (Figs 55–63) ..... ***petraeus*** (p. 233)
– Echemes repeated at the rate of about 2/s 3

3 Song consisting of about 11–15 echemes and lasting about 6–8 s (Figs 123–128) .... ***llorenteae*** (p. 243)
– Song consisting of about 6–10 echemes and lasting about 3–5 s (Figs 117–119) ***minutissimus*** (p. 243)

4 Song consisting of a single echeme lasting more than 4 s 5
– Song consisting of one or more echemes, each lasting less than 4 s 6

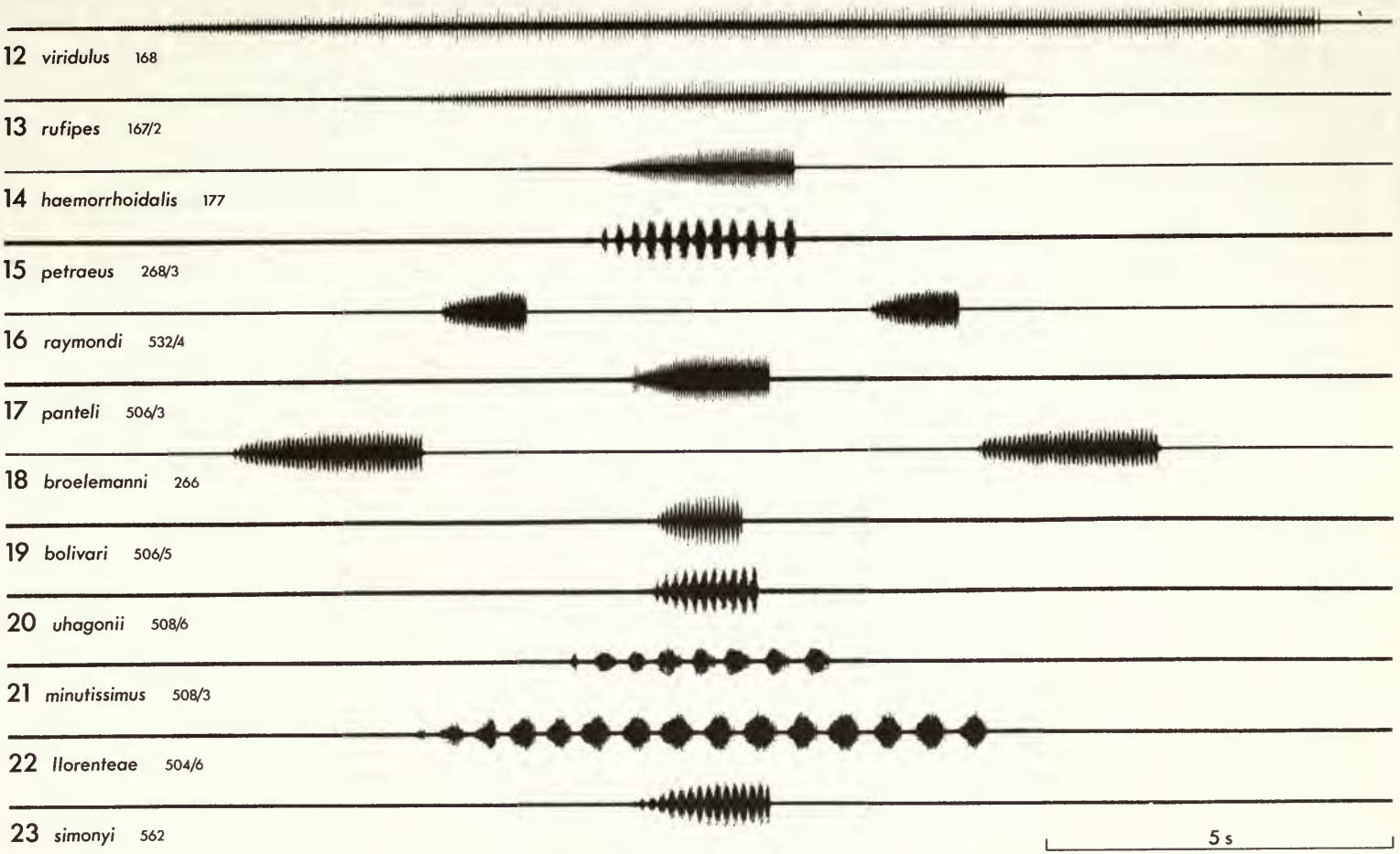
5 Echeme lasting more than 12 s (Figs 24–33) ..... ***viridulus*** (p. 226)
– Echeme lasting less than 12 s (Figs 34–45) ..... ***rufipes*** (p. 227)

6 Syllable repetition rate less than 10/s 7
– Syllable repetition rate more than 10/s 8

7 Each syllable with more than 7 gaps (Figs 108–116). (Iberian Peninsula) ..... ***uhagonii*** (p. 237)
– Each syllable with fewer than 6 gaps (Figs 120–122). (Canary Islands) ..... ***simonyi*** (p. 246)

8 Syllable repetition rate less than 20/s 9
– Syllable repetition rate more than 20/s 11

9 Echeme lasting more than 2 s (Figs 90–98) ..... ***broelemanni*** (p. 236)
– Echeme lasting less than 2 s (Figs 64–72 or 99–107) 10



Figs 12–23 Oscillograms of typical male calling songs of species of *Omocestus*. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).

10 Gaps becoming obscured towards the end of the echeme (Figs 64–72). (Widespread in Iberian Peninsula, S. France, NW. Italy and North Africa) ..... ***raymondi*** (p. 233)
– Gaps persisting to the end of the echeme (Figs 99–107). (Known only from the higher parts of the Sierra Nevada in S. Spain) ..... ***bolivari*** (p. 237)

11 Echeme lasting more than 2 s (Figs 46–54) ..... ***haemorrhoidalis*** (p. 227)
– Echeme lasting less than 2 s (Figs 73–89) ..... ***panteli*** (p. 236)

The songs of the western European *Omocestus*

Omocestus viridulus (Linnaeus)

(Figs 2, 6, 24–33)

Gryllus Locusta viridulus Linnaeus, 1758: 433. Lectotype ♂, SWEDEN: Gotland, Burgsvik (Linnean Society of London), designated by Marshall (1983: 394) [examined].

REFERENCES TO SONG. **Oscillogram**: Elsner, 1974, 1975; Grein, 1984; Haskell, 1957, 1958; Kutsch, 1976; Kutsch & Schiolten, 1979; Loher & Broughton, 1955; Zhantiev, 1981. **Diagram**: Bellmann, 1985*a*; Duijm & Kruseman, 1983; Haskell, 1957; Holst, 1970; Jacobs, 1950, 1953; Ragge, 1965; Wallin, 1979. **Frequency information**: Haskell, 1957, 1958. **Musical notation**: Yersin, 1854. **Verbal description only**: Beier, 1956; Faber, 1928, 1953; Haskell, 1955; Harz, 1957; Skovmand & Pedersen, 1978, 1983; Weber, 1984; Weih, 1951. **Disc recording**: Grein, 1984; Ragge, Burton & Wade, 1965. **Cassette recording**: Bellmann, 1985*b*; Wallin, 1979.

RECOGNITION. Males of this common species may be easily distinguished from the rather similar species *rufipes* and *haemorrhoidalis* by the lack of any red colouring on the abdomen, and females by the conspicuously longer ovipositor (Fig. 2). Both sexes also lack the dark markings in the medial area of the fore wings that are normally present in the other two species, and the pronotal lateral carinae are usually much less incurved in the prozona (Fig. 6).

In the field the conspicuously loud calling song of the male provides an easy means of identifying this species. Although similar in the quality of sound to the songs of *rufipes* and *haemorrhoidalis*, the song of *viridulus* is more prolonged, usually lasting for more than 12 s.

SONG (Figs 24–33). The calling song is an echeme usually lasting about 12–25 s and consisting of syllables repeated at the rate of about 15–20/s. The echeme beings quietly (the first few leg movements producing no audible sound) and gradually increases in loudness until the maximum intensity is reached after a few seconds; the echeme then continues at a constant intensity until reaching an abrupt end. The syllable repetition rate is highest at the beginning of the echeme (usually 18–20/s), gradually lessening towards the end (when it is usually 15–18/s). The song is a conspicuous summer sound in much of the European countryside, louder than the songs of most other common grasshoppers.

In the presence of a female the male produces longer echemes, usually lasting more than 30 s and occasionally more than a minute; one of the hind legs is moved through a noticeably wider angle than the other and produces most of the sound. After a series of these echemes with short pauses (about 10–15 s) between them, there is a quite different and much quieter echeme lasting about 3–5 s and composed of syllables repeated at the rate of about 12–16/s (Fig. 26). This is normally followed by a series of loud syllables and an attempt to copulate with the female. If this attempt is unsuccessful the male will usually produce a series of sharp 'ticks' (Fig. 27) by kicking backwards with the hind tibiae (as in the calling song of *Stethophyma grossum* (Linnaeus)) before beginning another sequence of courtship echemes. Usually the two hind tibiae are kicked simultaneously, but sometimes one at a time, changing haphazardly (rarely regularly) from one side to the other. The number of ticks is very variable but is usually between 5 and 15, and the repetition rate is rather irregular, generally about 1–2/s.

DISTRIBUTION. This common species occurs in fairly moist habitats throughout Europe, except for the extreme north and the southern parts of the Iberian, Italian and Balkan peninsulas; its range extends eastwards to Siberia and Mongolia.

Omocestus rufipes (Zetterstedt)

(Figs 3, 7, 34–45)

Gryllus rufipes Zetterstedt, 1821: 90. LECTOTYPE ♂, SWEDEN: Östergötland, Lärketorp (ZI, Lund), here designated (see p. 220) [examined]. [Validity established by von Borck (1848: 124) under Article 24 of the *International Code of Zoological Nomenclature*.]

Gryllus ventralis Zetterstedt, 1821: 89. Holotype ♀, SWEDEN: Skåne, near Tranås, Äsperöd ['Esperöd'] (ZI, Lund) [examined].

REFERENCES TO SONG. **Oscillogram**: Broughton, 1955; Grein, 1984; Loher & Broughton, 1955; Schmidt & Baumgarten, 1977. **Diagram**: Bellmann, 1985*a*; Duijm & Kruseman, 1983; Holst, 1970; Jacobs, 1950, 1953; Luquet, 1978; Ragge, 1965; Wallin, 1979. **Frequency information**: Busnel, 1955; Loher & Broughton, 1955. **Musical notation**: Yersin, 1854. **Verbal description only**: Beier, 1956; Chopard, 1922; Faber, 1953; Harz, 1957; Weih, 1951. **Disc recording**: Andrieu & Dumortier, 1963; Grein, 1984; Ragge, Burton & Wade, 1965. **Cassette recording**: Bellmann, 1985*b*; Wallin, 1979.

RECOGNITION. The red colouring on the underside of the abdomen and the conspicuously pale-tipped palps enable both sexes of this species to be distinguished from its relatives. The distal part of the hind wings is much more strongly smoky than in *haemorrhoidalis*, in which the male abdomen is occasionally reddish on the underside.

In the field the calling song of the males enables them to be recognized easily. Although quite similar in basic pattern to those of *viridulus* and *haemorrhoidalis*, the song of *rufipes* differs in duration, lasting about half as long as that of *viridulus* and about three times as long as that of *haemorrhoidalis*.

SONG (Figs 34–45). The calling song is an echeme usually lasting 5–10 s and consisting of syllables repeated at the rate of about 13–23/s. The echeme begins quietly and gradually increases in loudness until reaching an abrupt end, thus resembling the first half of the calling song of *viridulus*. As in *viridulus* the syllable repetition rate is highest at the beginning of the echeme (usually 17–23/s), gradually lessening towards the end (when it is usually 13–17/s).

In the presence of a female the male produces a courtship song quite similar to that of *viridulus*. There is first a series of echemes similar to those of the calling song but usually rather longer; this is followed by a quite different and quieter echeme lasting about 5–10 s and composed of syllables repeated at the rate of about 10–15/s (Fig. 37). There are then several loud syllables followed by an attempt to copulate with the female. The 'ticks' produced by backward kicks of the hind tibiae during the courtship song of *viridulus* seem never to occur in that of *rufipes*.

DISTRIBUTION. This species can tolerate drier conditions than *viridulus* and often occurs in more shaded habitats. Its distribution is very similar, but extends further south in the Iberian, Italian and Balkan peninsulas.

Omocestus haemorrhoidalis (Charpentier)

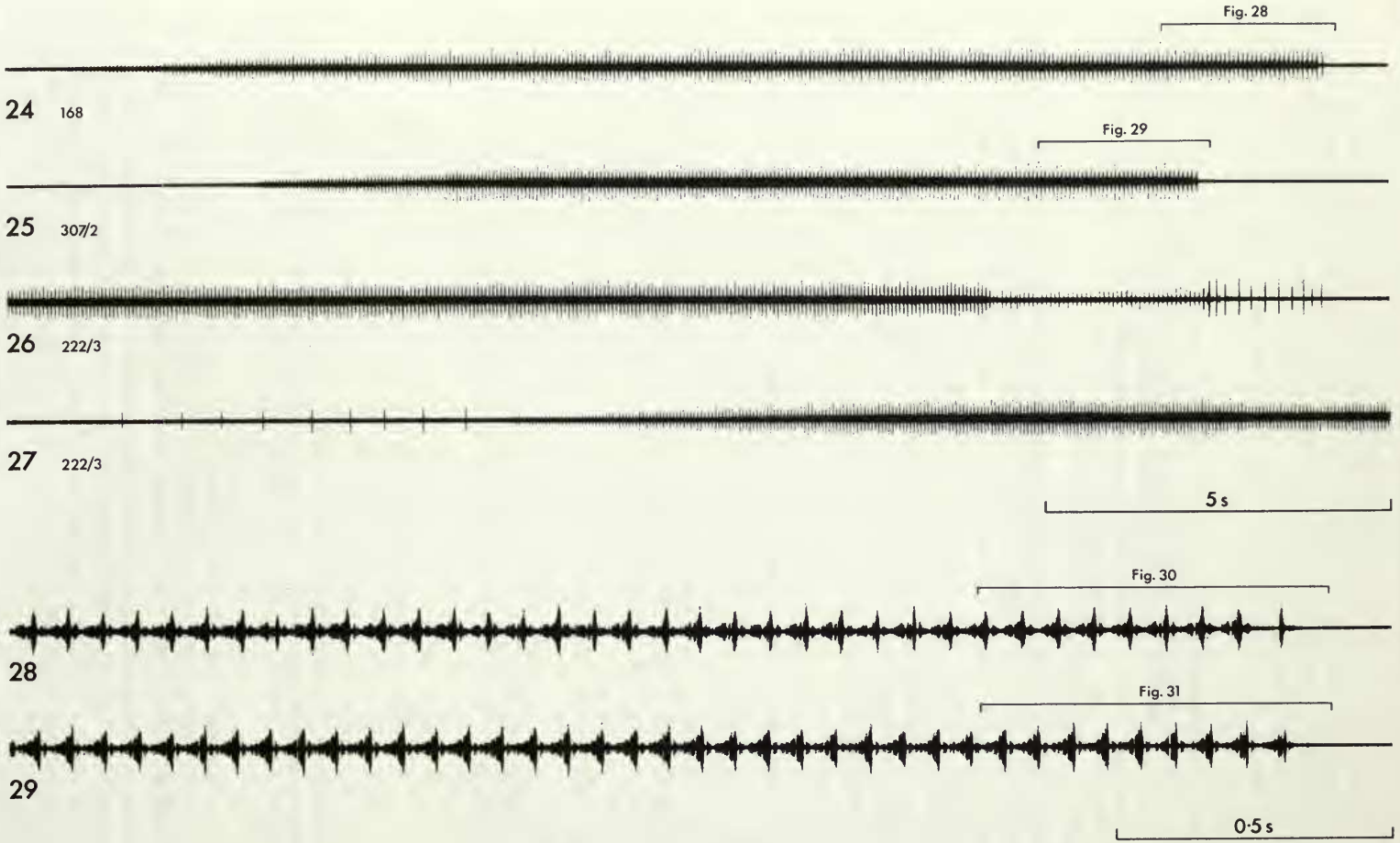
(Figs 8, 46–54)

Gryllus haemorrhoidalis Charpentier, 1825: 165. Syntypes of both sexes, POLAND/CZECHOSLOVAKIA: 'Silesia'. There are a male (in bad condition) and two females in the MNHU, Berlin that have been regarded as syntypes of this species, but none is labelled 'Silesia' and there is some doubt that they belong to the type-series.

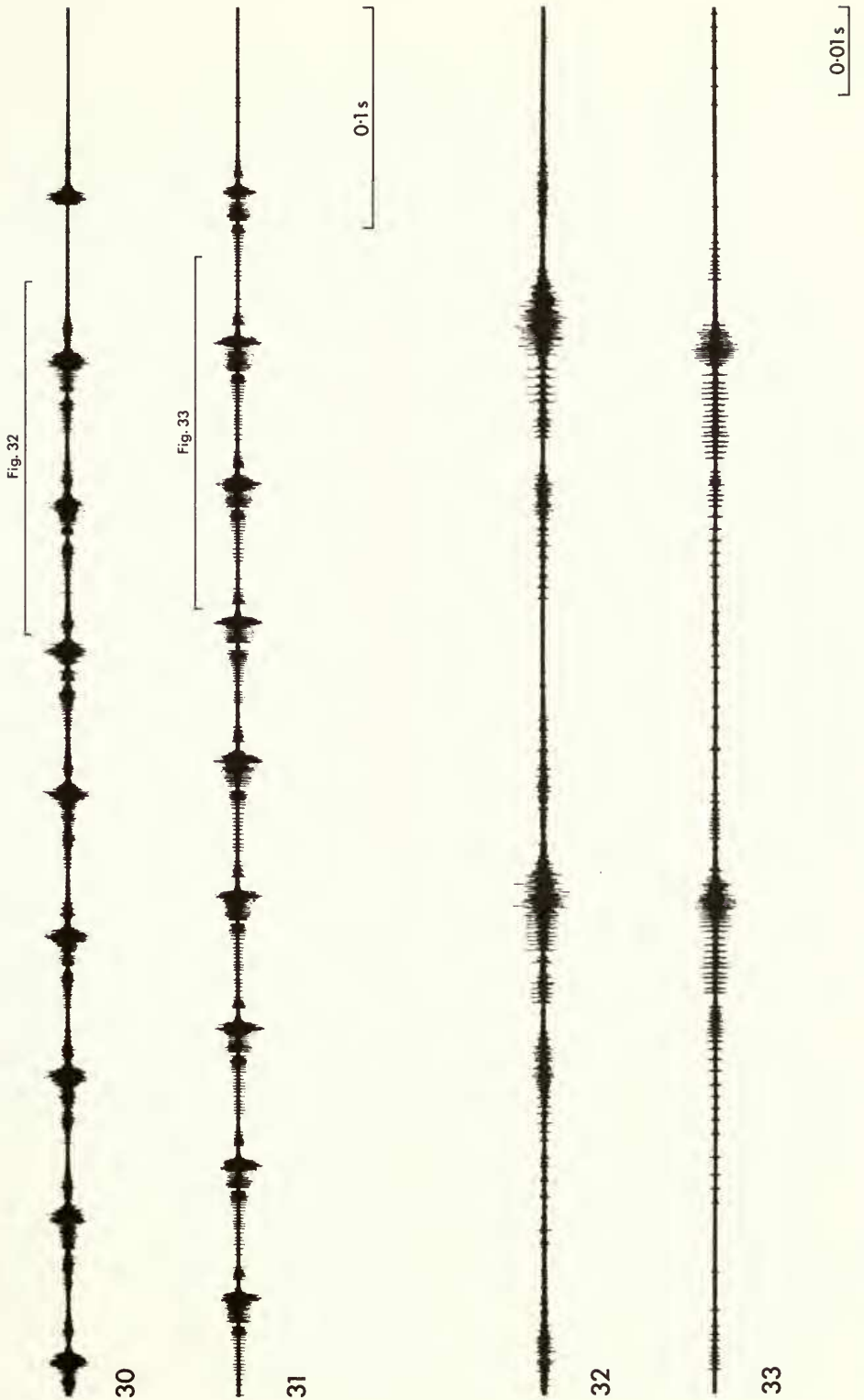
REFERENCES TO SONG. **Oscillogram**: Grein, 1984; Schmidt & Schach, 1978. **Diagram**: Bellmann, 1985*a*; Duijm & Kruseman, 1983; Jacobs, 1950, 1953; Wallin, 1979. **Verbal description only**: Faber, 1953; Harz, 1957; Weber, 1984. **Disc recording**: Grein, 1984. **Cassette recording**: Bellmann, 1985*b*; Wallin, 1979.

RECOGNITION. For the distinction between this species and *petraeus* see the remarks under that species. Both sexes may be distinguished from *viridulus, rufipes* and *raymondi* by the almost transparent hind wings (strongly smoky in the distal part in those three species). In the field the males can be recognized quite easily by their calling song, in which the echemes are shorter than those of *viridulus* and *rufipes*, but much longer than those of *raymondi*.

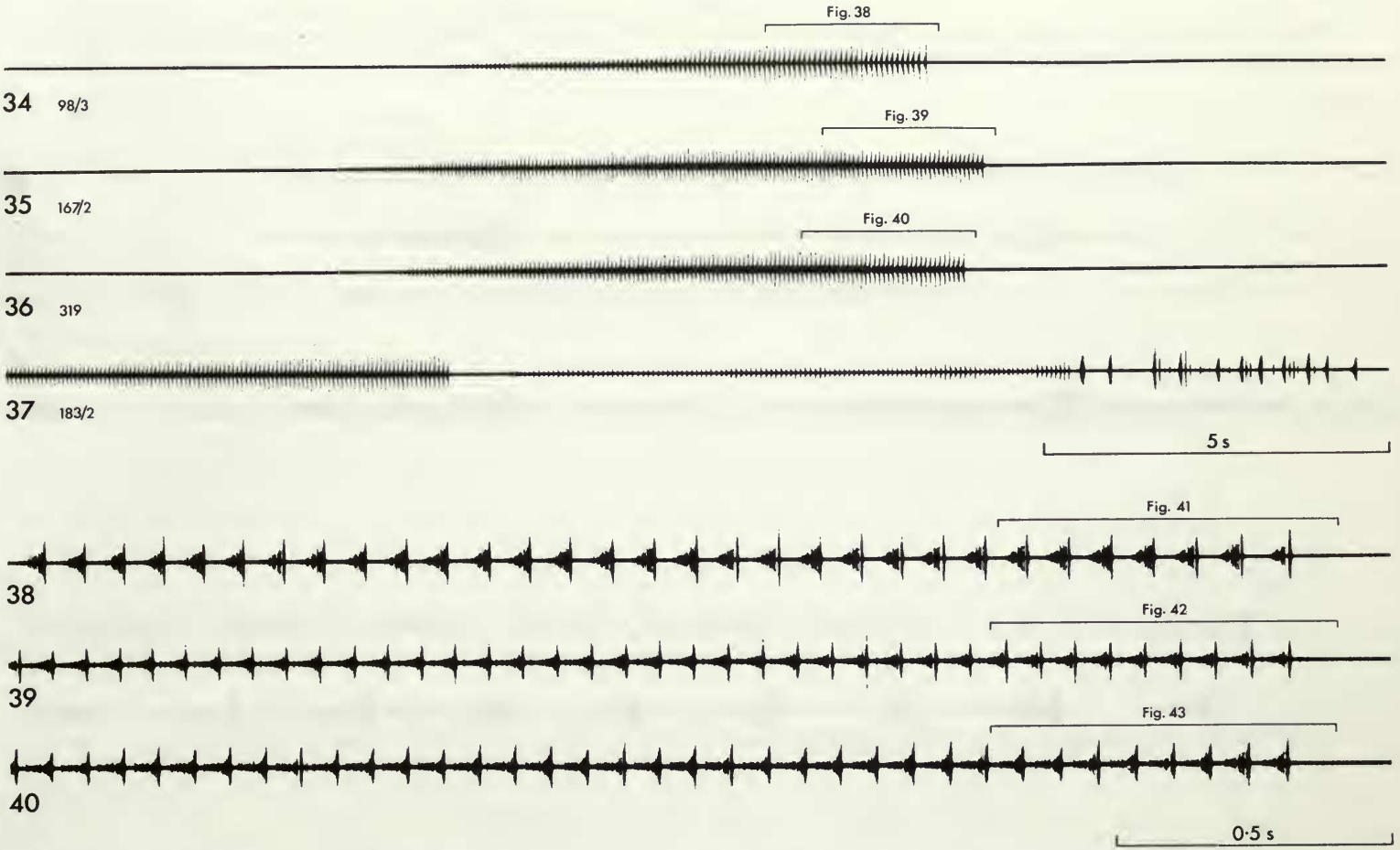
SONG (Figs 46–54). The calling song is an echeme lasting about 2–4 s and consisting of syllables



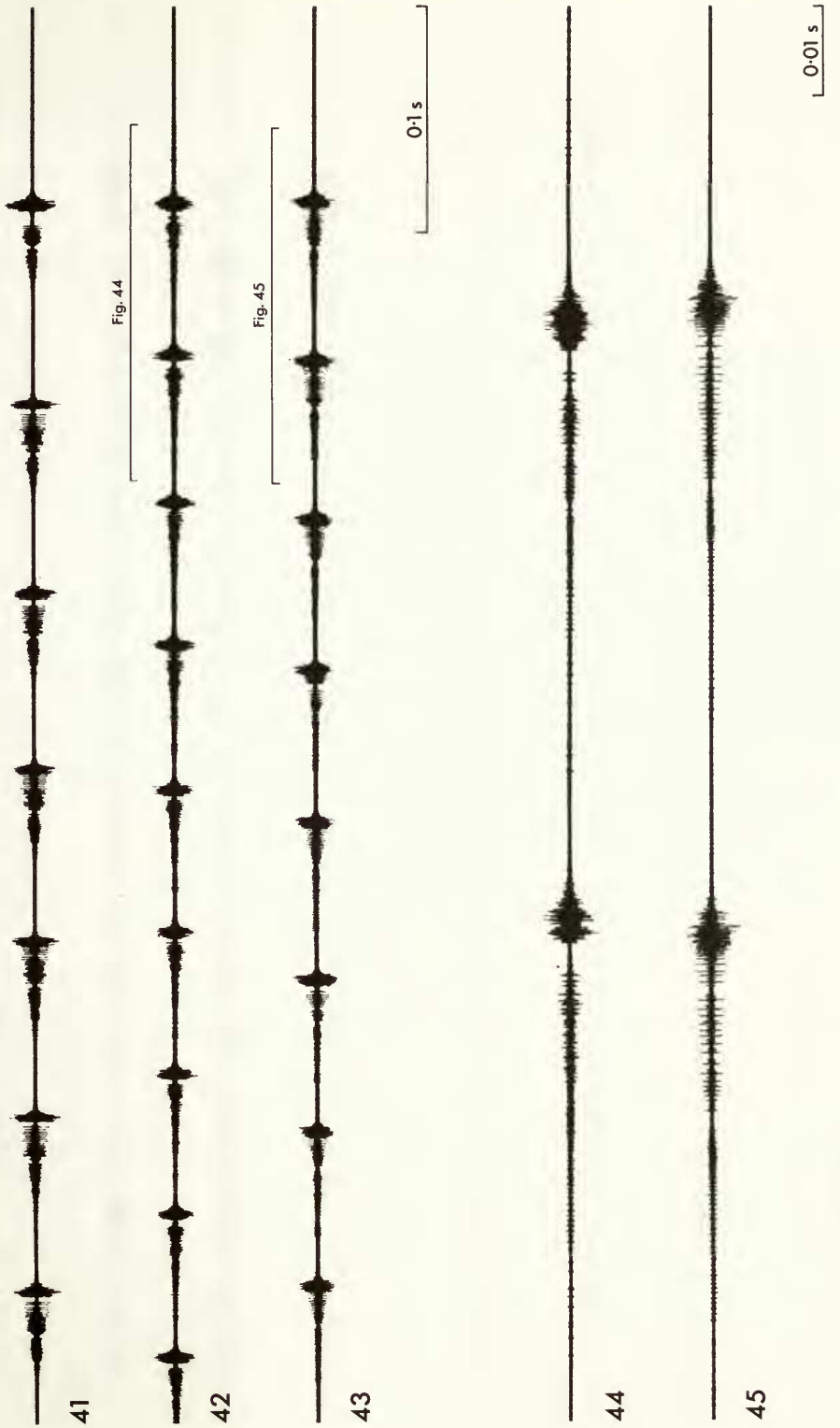
Figs 24–29 Oscillograms of the songs of three males of *Omocestus viridulus*. 24, 25. Calling songs of males with (24) two hind legs and (25) one hind leg. 26, 27. Parts of the courtship song showing (26) the concluding part of a main echeme followed by the quieter echeme and loud syllables that precede an attempt to copulate, and (27) the 'ticks' produced before the beginning of a main echeme. 28, 29. Faster oscillograms of the indicated parts of the songs shown in Figs 24, 25. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).



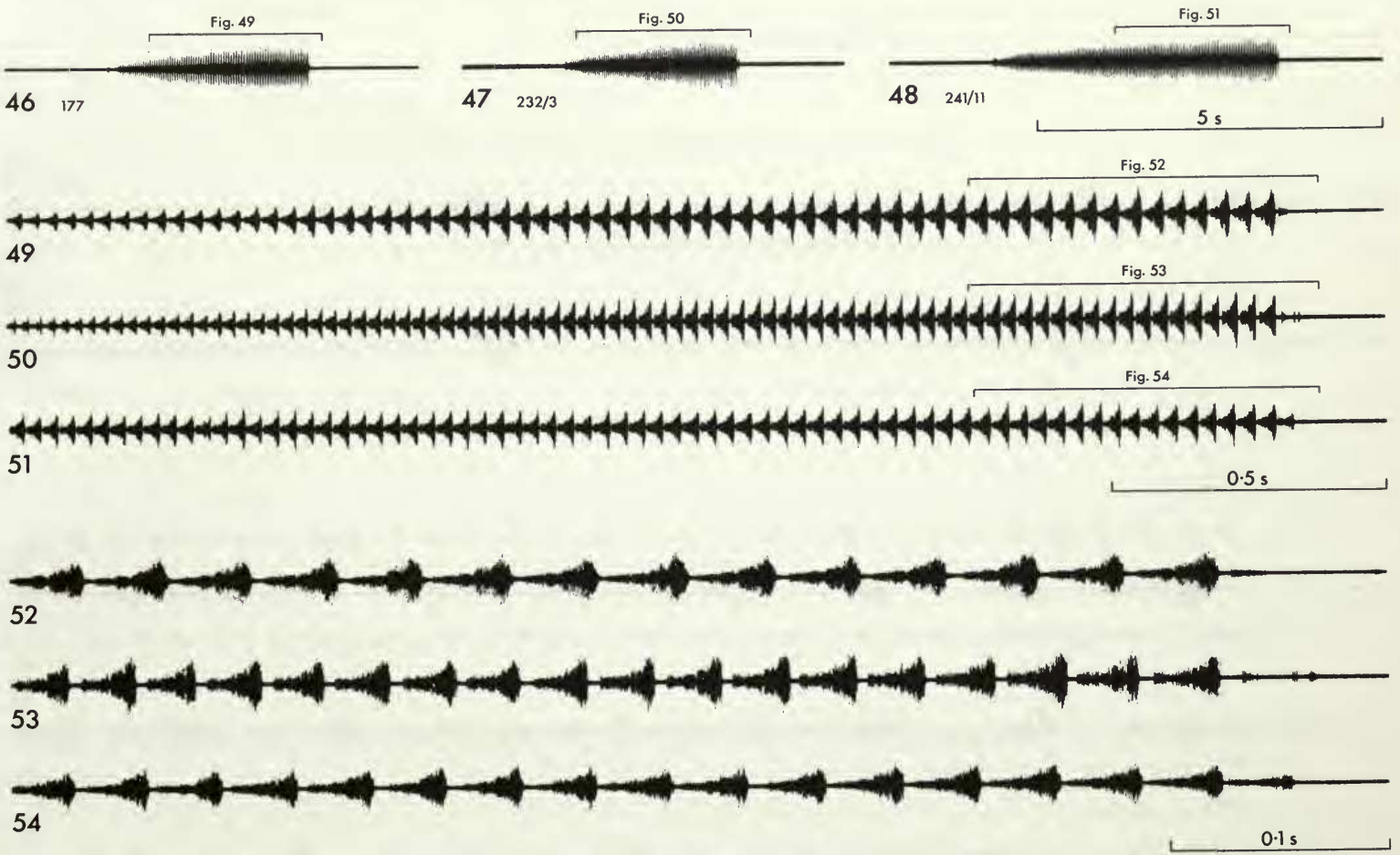
Figs 30–33 Faster oscillograms of the indicated parts of the songs of *Omocestus viridulus* shown in Figs 28, 29, showing the difference between the songs of males with (30, 32) two hind legs and (31, 33) one hind leg.



Figs 34–40 Oscillograms of the songs of four males of *Omocestus rufipes*. 34–36. Calling songs of males with (34, 35) two hind legs and (36) one hind leg. 37. Part of the courtship song showing the concluding part of a main echeme followed by the quieter echeme and loud syllables that precede an attempt to copulate. 38–40. Faster oscillograms of the indicated parts of the songs shown in Figs 34–36. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).



Figs 41–45 Faster oscillograms of the indicated parts of the songs of *Omocestus rufipes* shown in Figs 38–40, showing the difference between the songs of males with (41, 42, 44) two hind legs and (43, 45) one hind leg.



Figs 46–54 Oscillograms at three different speeds of the calling songs of three males of *Omocestus haemorrhoidalis*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).

repeated at the rate of about 25–40/s (about double the rate of *viridulus* and *rufipes*). The echeme begins quietly but soon reaches maximum intensity. The syllable repetition rate gradually lessens during the course of the echeme.

DISTRIBUTION. Widely distributed in continental Europe, but not known from the Scandinavian mainland and limited to mountains in the southern peninsulas. The range extends eastwards across central Asia to Mongolia, Manchuria and Korea.

Omocestus petraeus (Brisout)

(Figs 9, 55–63)

Acridium petraeum Brisout, 1855: cxiv. LECTOTYPE ♂, FRANCE: near Paris, Lardy (*Brisout*) (IRSNB, Brussels), here designated (see p. 221) [examined].

REFERENCES TO SONG. **Diagram**: Luquet, 1978. **Verbal description only**: Faber, 1953; Harz, 1957.

RECOGNITION. This species lacks the smoky coloration of the distal part of the hind wings shown by *viridulus, rufipes* and *raymondi*, and is also noticeably smaller. Distinguishing it from *haemorrhoidalis* is more difficult, especially if reliably identified specimens of both species are not available for comparison. *O. petraeus* is again noticeably smaller, and the head is larger in comparison to the pronotum and more convex above with shorter foveolae. The males lack the red colouring shown by the distal part of the abdomen in *haemorrhoidalis*, showing a yellowish colouring in this region instead.

The highly distinctive calling song, consisting of about 10–20 rapidly repeated echemes, enables males of this species to be recognized easily in the field.

SONG (Figs 55–63). The calling song consists of a sequence of about 10–20 echemes lasting about 2–5 s. The sequence begins quietly, reaching maximum intensity after about 6 echemes; even at its maximum intensity the song is rather quiet. The echeme repetition rate is usually about 4/s, and the syllable repetition rate within each echeme about 80–110/s. Each of the louder echemes lasts for about 150 ms and contains about 10–15 syllables.

In the presence of a female the male produces echemes of a quite different kind (Figs 57, 60, 63). Each echeme begins with a relatively long syllable, lasting about 20–50 ms, and this is immediately followed by a series of very short sounds, each lasting less than 5 ms, repeated at the rate of about 50/s. These echemes are produced either singly or, more often, in groups of about 2–5.

DISTRIBUTION. Western, central and eastern Europe, Asia Minor and southern Siberia. Largely absent from the Iberian Peninsula, but quite widespread in Italy and the Balkan Peninsula.

Omocestus raymondi (Yersin)

(Figs 10, 64–72)

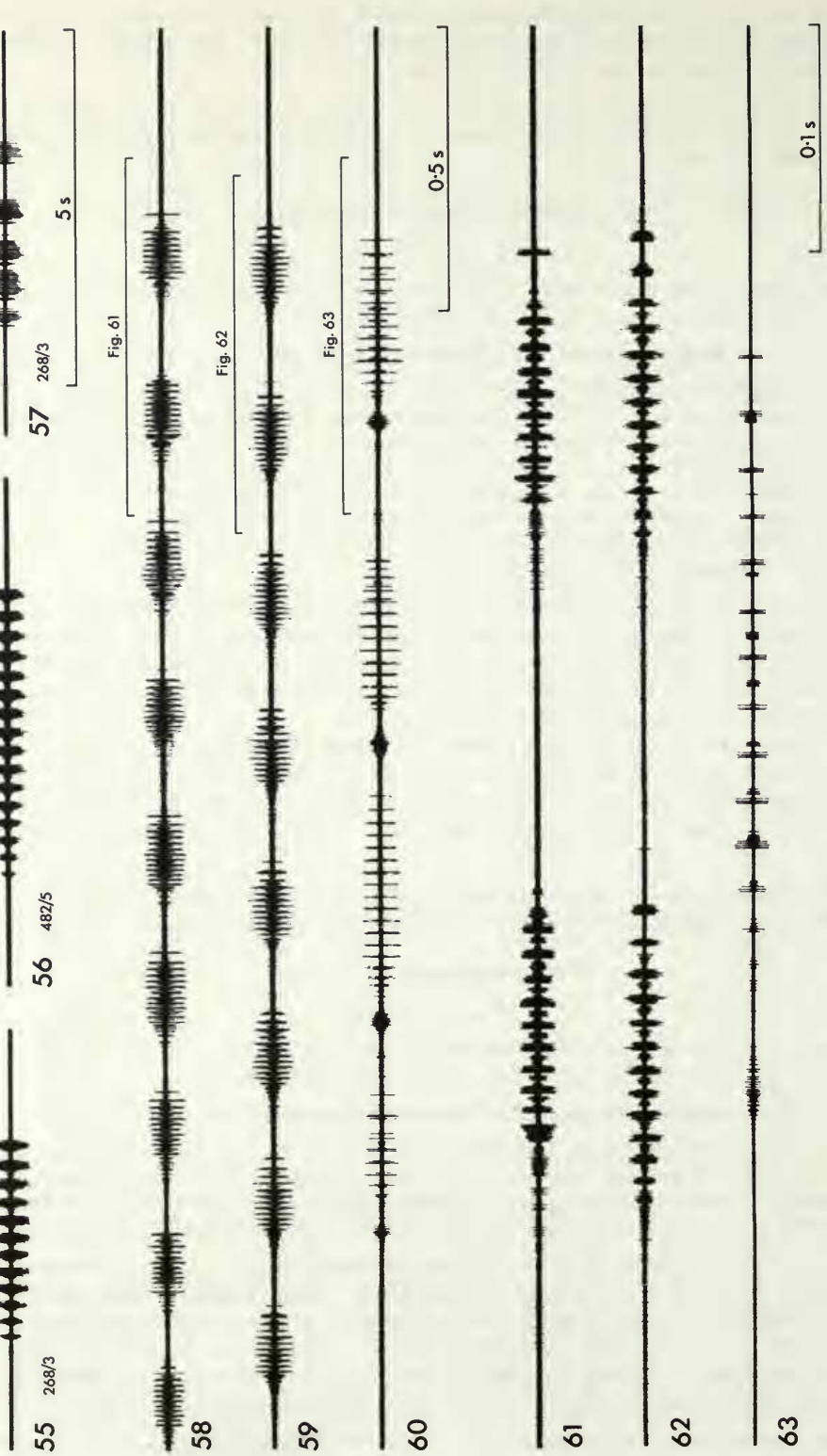
Stenobothrus raymondi Yersin, 1863: 289. Syntypes of both sexes, FRANCE: Var, near Hyères (*Raymond*) (lost); the two 'neotypes' designated by Harz (1975: 713) are clearly invalid.

REFERENCES TO SONG. **Diagram**: Luquet, 1978. **Verbal description only**: Chopard, 1922, 1952.

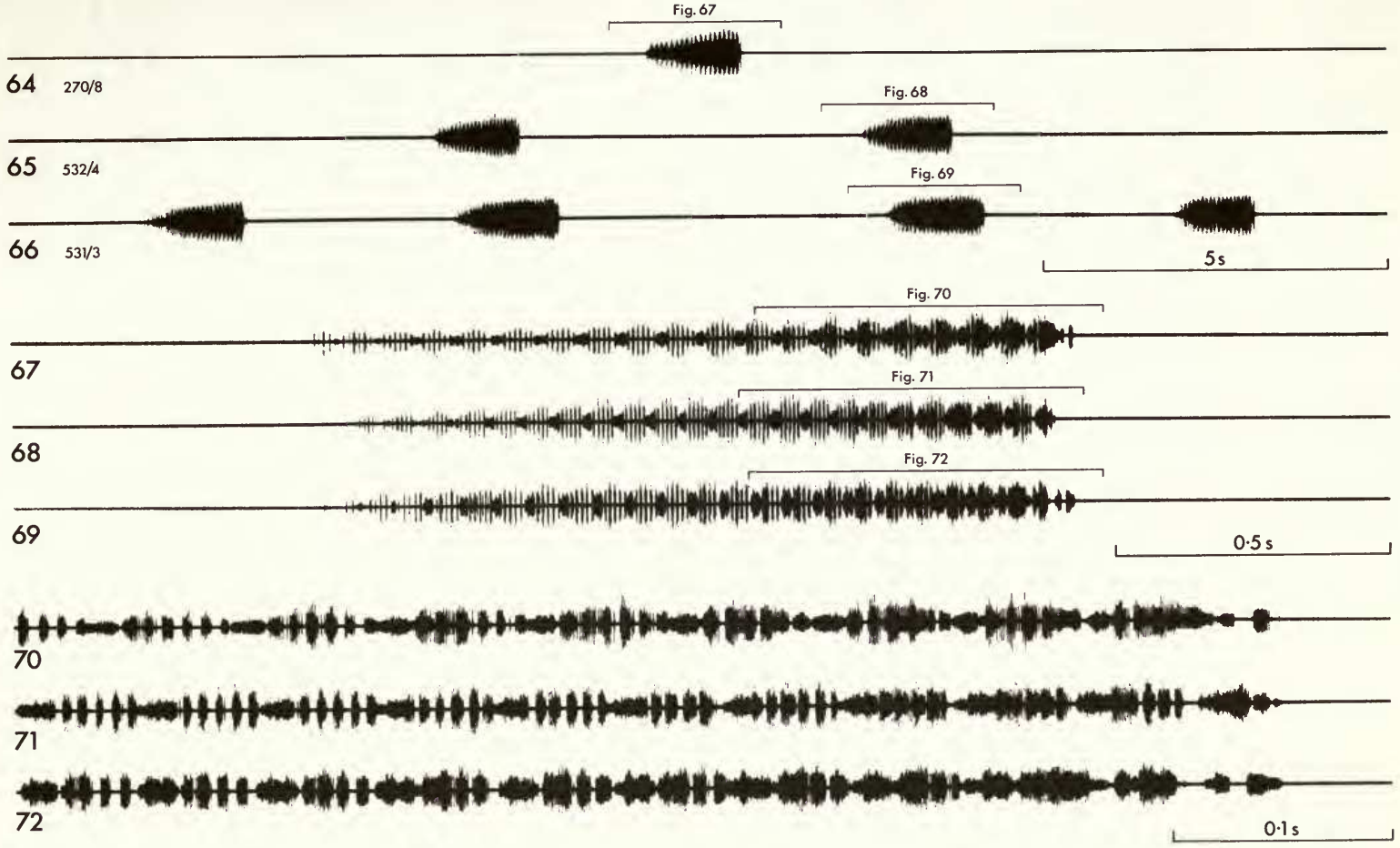
RECOGNITION. This all-brown species is most likely to be confused with *haemorrhoidalis*, but can be distinguished from it in both sexes by the strongly smoky distal part of the hind wings (almost transparent in *haemorrhoidalis*). In the field males may be distinguished from those of *haemorrhoidalis* by the very short echemes (lasting about 1 s) and slower syllable repetition rate (less than 20/s) of the calling song.

SONG (Figs 64–72). The calling song is an echeme lasting about 1·0–1·5 s and consisting of about 18–25 syllables repeated at the rate of 15–20/s. Each echeme usually begins quietly, rapidly increasing in intensity. Oscillograms show the syllables to have a characteristic pattern of gaps, which often becomes obscured towards the end of the echeme (Figs 67–69). The echemes are often produced singly and repeated at irregular intervals (10–15 s is typical), but sometimes they are in groups of 2–4 with much shorter intervals between them (often 2–5 s) (Figs 65, 66).

DISTRIBUTION. Known only from southern France, the Iberian Peninsula, north-western Italy and North Africa.



Figs 55–63 Oscillograms at three different speeds of the songs of two males of *Omocestus petraeus*. 55, 56, 58, 59, 61, 62. Calling songs. 57, 60, 63. Courtship song of the same male as Figs 55, 58, 61. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 216).



Figs 64–72 Oscillograms at three different speeds of the calling songs of three males of *Omocestus raymondi*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 216).

Omocestus panteli (Bolívar)

(Figs 11, 73–89)

Stenobothrus panteli Bolívar, 1887: 95. Syntypes of both sexes, SPAIN: Cuenca, near Uclés (?MNCN, Madrid).

REFERENCES TO SONG. No published work known to me.

RECOGNITION. In the Iberian Peninsula, to which it is confined, *panteli* is most likely to be confused with *viridulus*; it is, however, much smaller than that species and can be further distinguished from it by the red tip of the male abdomen and the relatively short ovipositor. There is also a superficial resemblance to *Stenobothrus stigmaticus* (Rambur), which is similar in size and also widespread in the Iberian Peninsula, but the pronotal lateral carinae are straighter in *panteli*, the male cerci are conical throughout (laterally compressed at the tip in *stigmaticus*) and the female lacks the teeth on the ovipositor shown by all species of *Stenobothrus*. There is a large form (var. *meridionalis* Bolívar) found in the south of the peninsula, especially in mountains; this form is even more like *viridulus*, but confusion is unlikely as that species does not occur in southern Spain.

In the field the song may be recognized by its short duration (less than 2 s) and high syllable repetition rate (usually more than 20/s).

SONG (Figs 73–89). The calling song is an echeme lasting 1–2 s and consisting of about 30–55 syllables repeated at the rate of about 18–30/s. The echeme begins quietly (sometimes after a few louder syllables) but soon reaches maximum intensity. The syllable repetition rate gradually lessens during the course of the echeme.

In the presence of a female the male first produces a different kind of echeme lasting about 2–3 s, and this is immediately followed by an echeme similar in duration and syllable repetition rate to that of the calling song but with an increase in intensity continuing through the whole echeme (Figs 77, 82, 87).

DISTRIBUTION. This species is confined to the Iberian Peninsula, where it is widespread and very common.

Omocestus broelemanni (Azam)

(Figs 90–98)

Stenobothrus Brölemanni Azam, 1906: 128. LECTOTYPE ♂, FRANCE: Pyrénées-Orientales, Val d'Eyne, 1700–2200 m, 14.viii.1905 (*Brölemann*) (MNHN, Paris), here designated (see p. 221) [examined].

REFERENCES TO SONG. **Oscillogram**: Reynolds, 1986.

RECOGNITION. This Pyrenean species is brachypterous, the fore wings not usually reaching the hind knees in the male and reduced to short lobes (about 1·5 times the length of the pronotum) in the female; in both sexes the hind wings fall short of the fore wings by quite a large gap. There is thus no risk of confusion with *viridulus, rufipes, haemorrhoidalis* and the other fully winged species of *Omocestus*. Confusion is also unlikely with the brachypterous species occurring further south in Spain, such as *uhagonii* and *minutissimus*, which are much smaller and not known from the vicinity of the Pyrenees. The relationship of *O. broelemanni* with *O. antigai* (Bolívar) and *O. navasi* Bolívar has been recently discussed by Reynolds (1986).

In the field the calling song of the male is quite distinctive, consisting of echemes lasting about as long as those of *haemorrhoidalis* but with about half the syllable repetition rate of that species.

SONG (Figs 90–98). The calling song, recently described for the first time by Reynolds (1986), is a series of echemes, each lasting about 1·5–3·0 s and consisting of about 25–45 syllables repeated at the rate of about 15–16/s. Each echeme begins quietly, reaching maximum intensity after about 1 s. Although the echemes are sometimes produced singly, they are more often repeated fairly regularly, about every 5–10 s, in a series of indefinite duration.

During the courtship song, which has also been described by Reynolds (1986), the male often produces a series of rather longer echemes (each lasting up to 5 s) and this is followed by a variable number of short echemes of small numbers of syllables (or even single syllables)

produced by one leg only (Figs 92, 95, 98). There is then a series of single syllables produced by both legs, followed by an attempt at copulation.

DISTRIBUTION. Known only from the vicinity of the Pyrenees, particularly the eastern end of the range.

Omocestus bolivari Chopard

(Figs 99–107)

Omocestus Bolivari Chopard, 1939: 172. LECTOTYPE ♂, SPAIN: Granada, Sierra Nevada, slopes of Mulhacén, 3000 m ['2000 m. environ' according to Chopard, *loc. cit.*], 10.vii.1934 (*Balachowsky*) (MNHN, Paris), here designated (see p. 221) [examined].

REFERENCES TO SONG. No published work known to me.

RECOGNITION. This species, known only from the higher parts of the Sierra Nevada in southern Spain, is very similar to *uhagonii, llorenteae* and *minutissimus*. Males may be distinguished from all three of these species by their short hind wings, which are less than half the length of the fore wings, and the females by their short fore wings, which are usually less than 1·3 times longer than the pronotum.

In the field the isolated echemes of the calling song enable males to be easily distinguished from *llorenteae* and *minutissimus*; from *uhagonii* they may be distinguished by the much faster syllable repetition rate.

SONG (Figs 99–107). The calling song is an echeme lasting 0·5–2·0 s and consisting of about 10–30 syllables repeated at the rate of 14–16/s. Each echeme begins quietly, soon reaching maximum intensity. Oscillographic analysis shows that there are gaps in each syllable (mainly in the later part of the syllable) and that they occur throughout the echeme; there are, however, only 2–4 gaps per syllable (Figs 102–107), many fewer than in *uhagonii*. As in *uhagonii* the echemes are repeated at irregular intervals, varying from a few seconds to over a minute.

DISTRIBUTION. Known only from the higher parts of the Sierra Nevada in southern Spain, usually at altitudes above 1500 m.

Omocestus uhagonii (Bolívar)

(Figs 4, 108–116)

Gomphocerus (Stenobothrus) Uhagonii Bolívar, 1876: 324. LECTOTYPE ♂, SPAIN: Madrid, Navarredonda (*Avila*) (MNCN, Madrid), here designated (see p. 221) [examined].

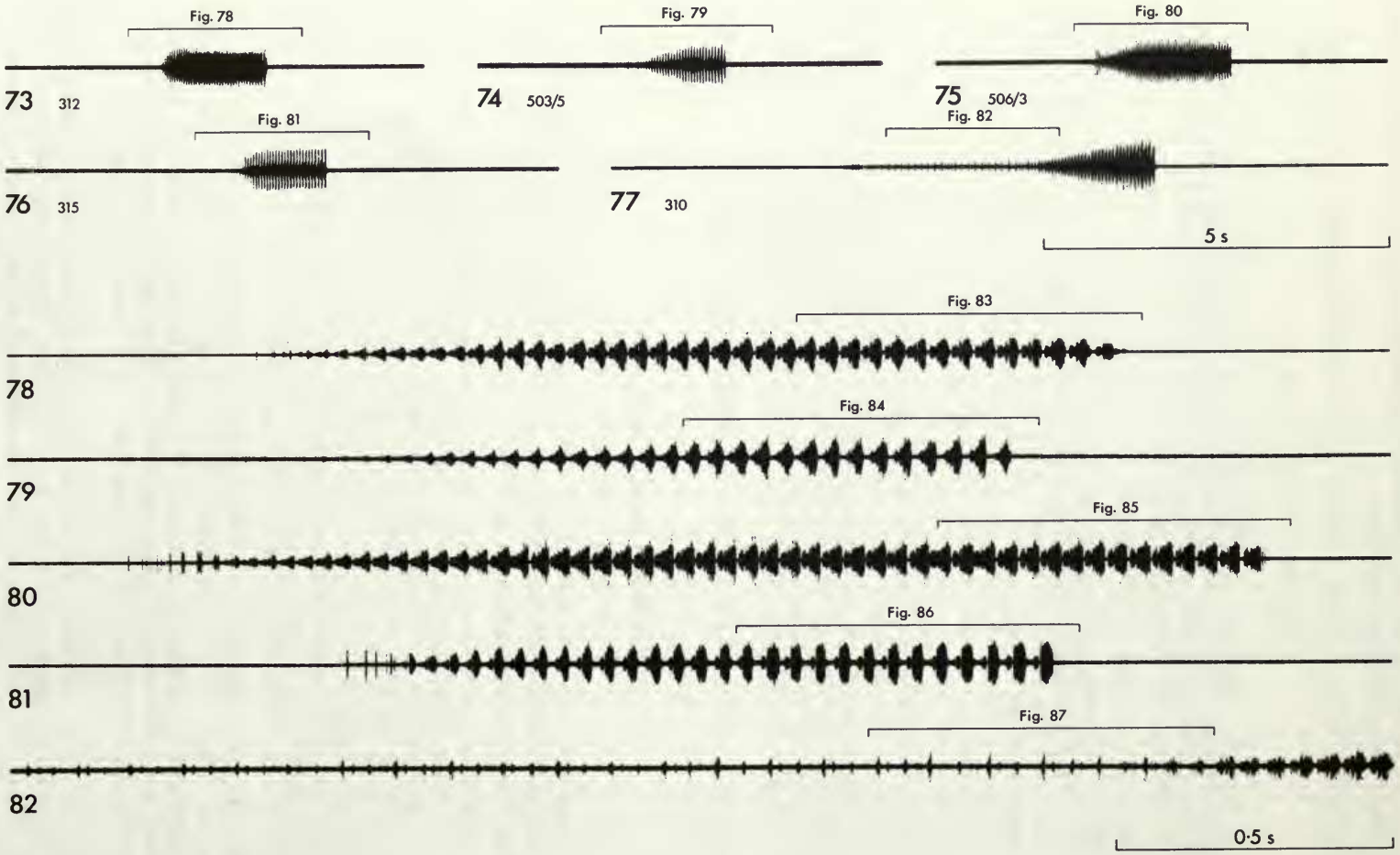
REFERENCES TO SONG. No published work known to me.

RECOGNITION. Males of this brachypterous montane species can be distinguished from the rather similar species *bolivari, llorenteae* and *minutissimus* by the cerci, which are laterally compressed towards the tip (simply conical in the other three species). Females can be separated from *bolivari* and *llorenteae* by the length of the fore wings, which are 1·4–1·8 times longer than the pronotum (the corresponding ratios for *bolivari* and *llorenteae* are 0·9–1·3 and 2·1–2·5, respectively), and from *minutissimus* by the much less strongly sigmoid ventral profile of the lower valves of the ovipositor (*cf.* Figs 4, 5).

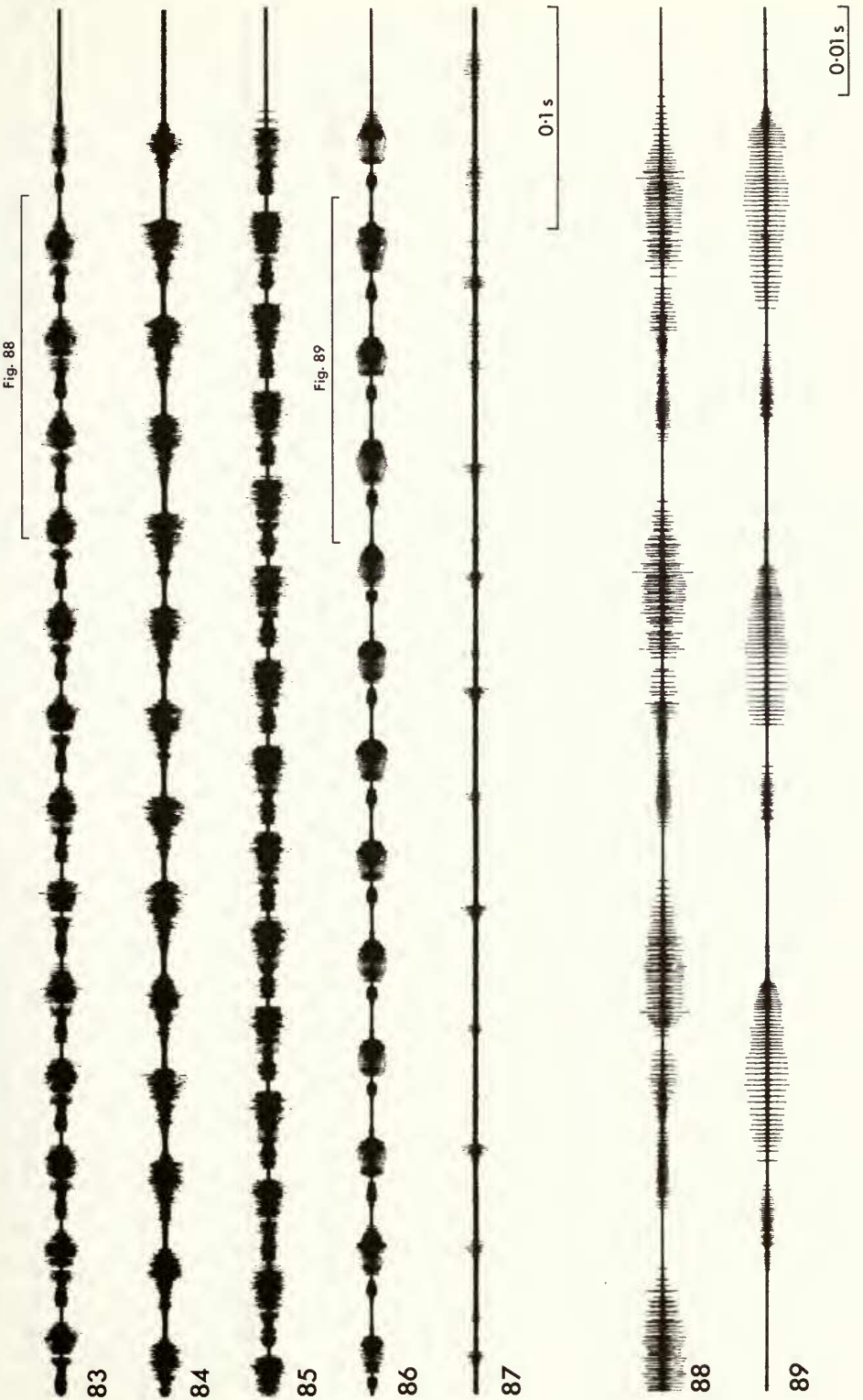
In the field the calling song of the males enables this species to be easily distinguished from *llorenteae* and *minutissimus*, which produce echeme-sequences of a quite different kind (*cf.* Figs 20–22); from *bolivari* it may be distinguished by the much slower syllable repetition rate (*cf.* Figs 19, 20).

SONG (Figs 108–116). The calling song is an echeme lasting 1–2 s and consisting of about 10–15 syllables repeated at the rate of 6–7/s. Each echeme begins quietly, rapidly increasing in intensity. Oscillographic analysis shows that each syllable has a large number of gaps (commonly as many as 8) and that this pattern of gaps is maintained until the end of the echeme (Figs 111, 112). The echemes are repeated at irregular intervals, varying from a few seconds to over a minute.

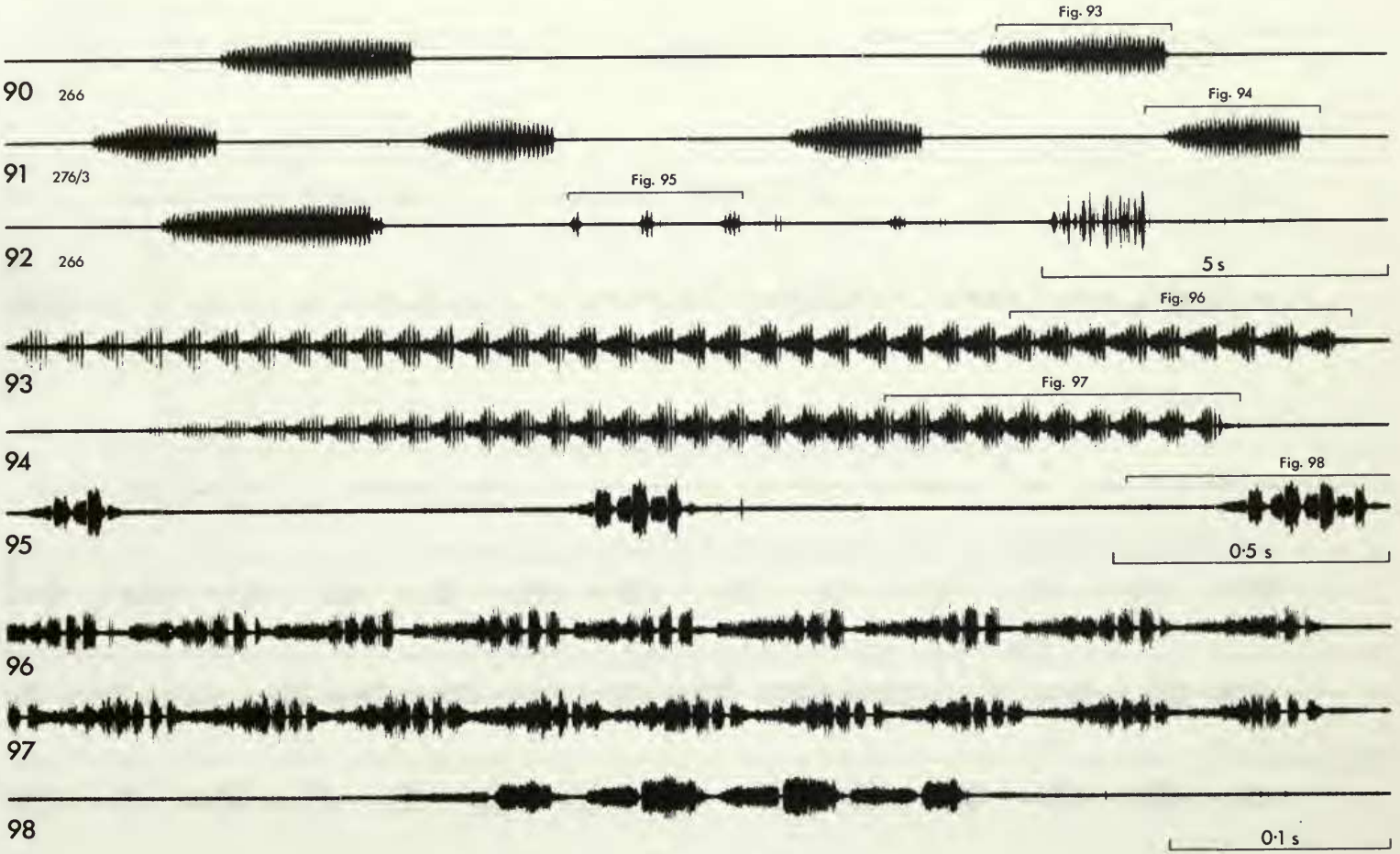
In the presence of a female the male produces a series of slightly longer echemes (lasting 2–3 s) at much more regular intervals (usually 6–8 in 40 s) (Fig. 110). The echemes consist of about 15–20 syllables and at the end of some of them (usually about half) there is a group of 3–4 syllables of a different kind (Figs 113, 116), repeated more rapidly (at the rate of about 16/s). In



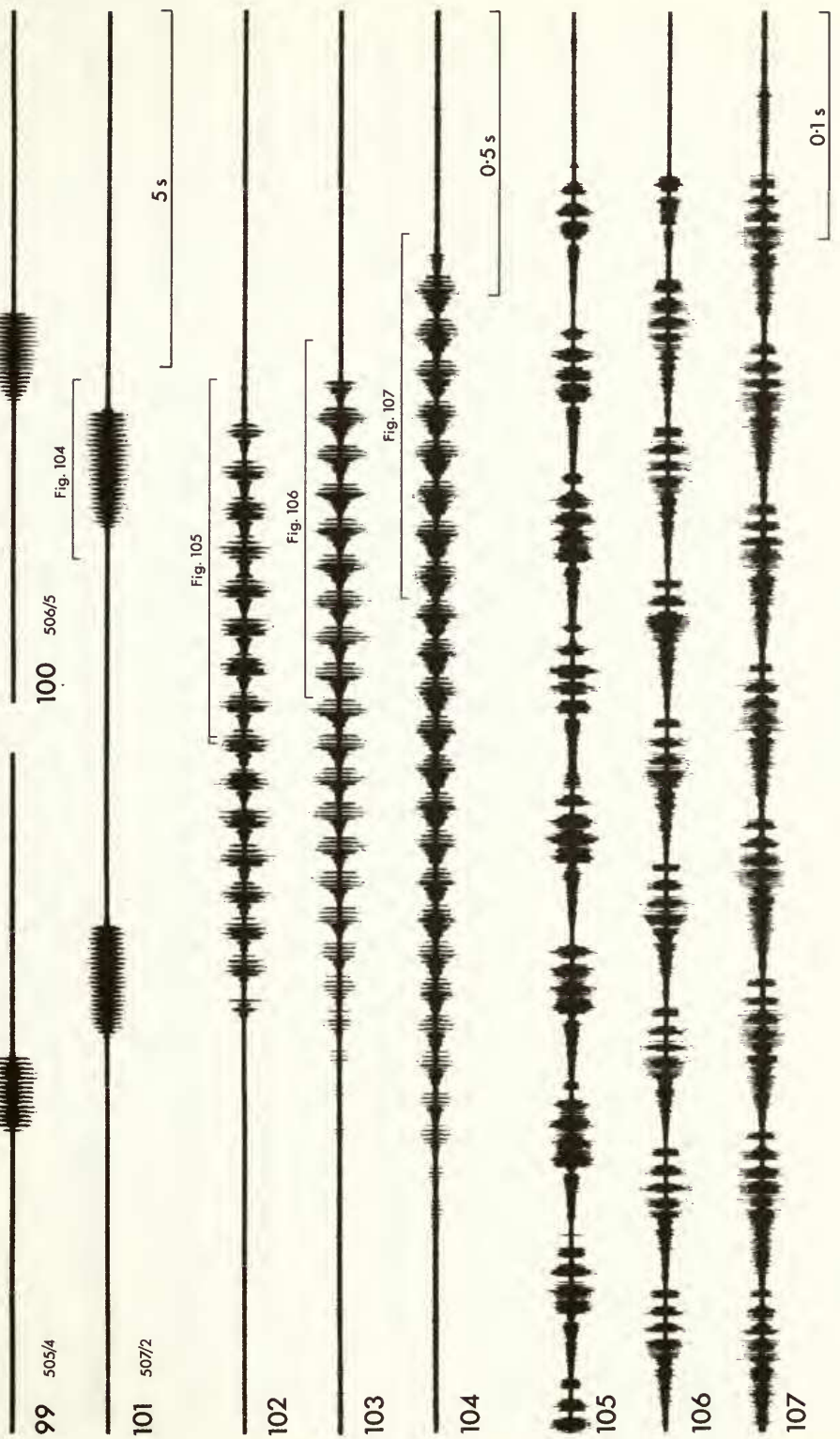
Figs 73–82 Oscillograms of the songs of five males of *Omocestus panteli*. 73–76. Calling songs of males with (73–75) two hind legs and (76) one hind leg. 77. Courtship song. 78–82. Faster oscillograms of the indicated parts of the songs shown in Figs 73–77. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).



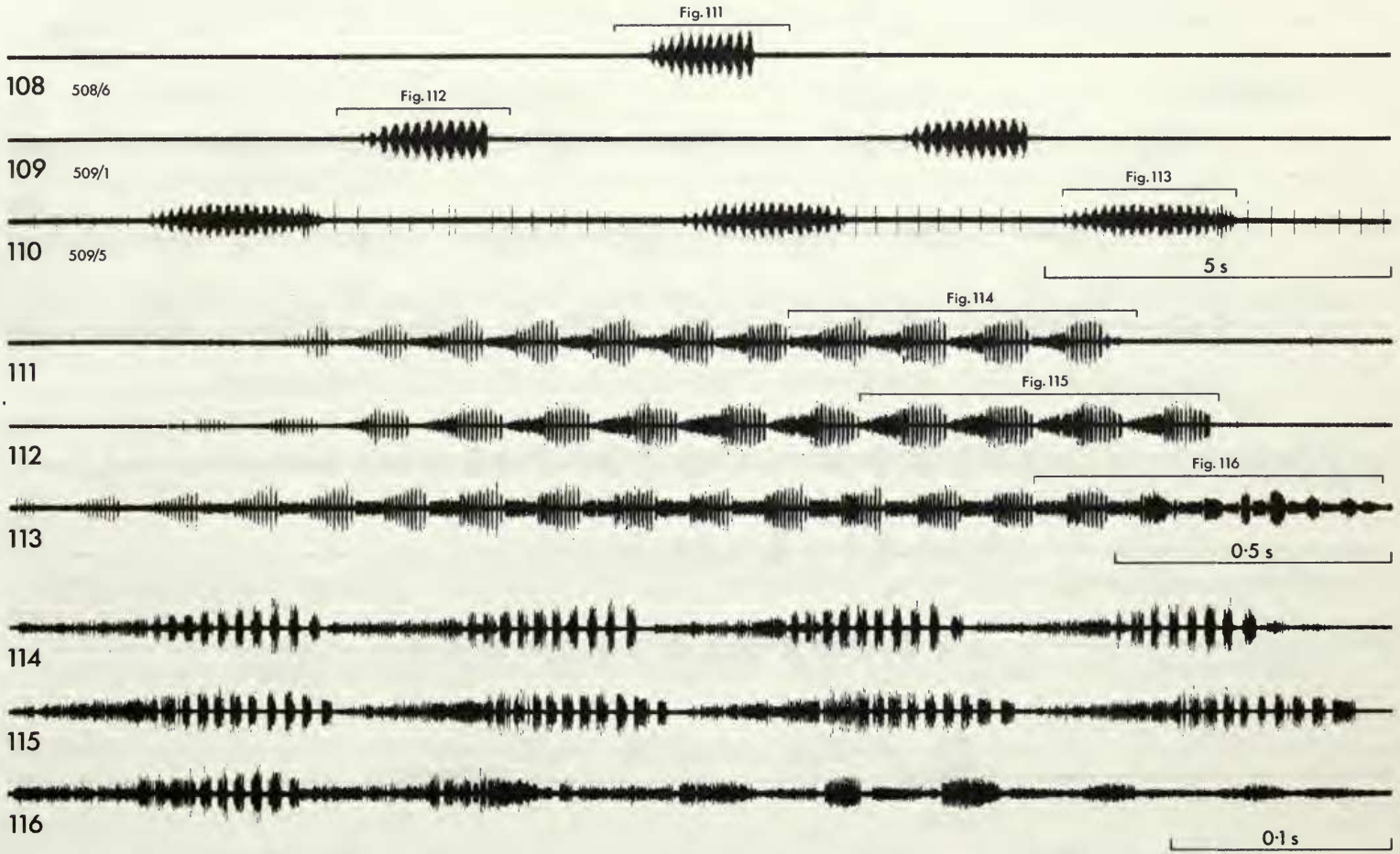
Figs 83–89 Faster oscillograms of the indicated parts of the songs of *Omocestus panteli* shown in Figs 78–82. Figs 86 and 89 are from a male with only one hind leg (see p. 219).



Figs 90–98 Oscillograms at three different speeds of the songs of two males of *Omocestus broelemanni*. 90, 91, 93, 94, 96, 97. Calling songs. 92, 95, 98. Courtship song of the same male as Figs 90, 93, 96. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).



Figs 99–107 Oscillograms at three different speeds of the calling songs of three males of *Omocestus bolivari*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 216).



Figs 108–116 Oscillograms at three different speeds of the songs of three males of *Omocestus uhagonii*. 108, 109, 111, 112, 114, 115. Calling songs. 110, 113, 116. Part of the courtship song. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 217).

the intervals between the echemes there are quieter 'ticking' sounds repeated fairly regularly at the rate of about 3–4/s. The number of echemes in the series is variable but can be more than 20. The series of echemes is followed by a variable period (often more than a minute) in which the quiet ticking continues and which ends in a number of sequences of a different kind of sound, still quiet, and then an attempt at copulation. If this is unsuccessful the cycle begins again with another series of echemes.

DISTRIBUTION. This species has been previously known only from the mountains of central and northern Spain, but my wife and I collected a series of adults of both sexes at El Chorillo (2700 m), south of the Mulhacén peak in the Sierra Nevada, on 31 July 1983.

Omocestus minutissimus (Bolívar)

(Figs 5, 117–119)

Gomphocerus (Omocestus) minutissimus Bolívar, 1878: 424. Syntypes of both sexes, SPAIN: Navarra, Cascante (*Perez Arcas*); Madrid, Escorial (MNCN, Madrid; BMNH, London; probably other depositories) [♀ syntype from Escorial in BMNH examined].

REFERENCES TO SONG. No published work known to me.

RECOGNITION. Males of this small upland species may be distinguished from *uhagonii* by the cerci, which are simply conical (laterally compressed towards the tip in *uhagonii*). They can be separated from *bolivari* and *llorenteae* by the length of the hind wings, which are more than half the length of the fore wings but do not reach the fore wing-tips. Females can be distinguished from *bolivari* and *llorenteae* by the length of the fore wings, which are usually 1·4–2·1 times the length of the pronotum; the corresponding ratios for *bolivari* and *llorenteae* are 0.9–1·3 and 2·1–2·5, respectively (these two species are in any case known only from the Sierra Nevada or Sierra Espuña, where *minutissimus* does not apparently occur). Females of *minutissimus* may be separated from those of *uhagonii* by the strongly sigmoid ventral profile of the lower valves of the ovipositor (*cf.* Figs 4, 5).

In the field the calling song of the males, consisting of a rapid sequence of echemes, enables this species to be easily distinguished from *uhagonii* and *bolivari*; from *llorenteae* it may be distinguished by being shorter (usually lasting less than 6 s) and having fewer echemes in each sequence (usually fewer than 10).

SONG (Figs 117–119). The rather quiet calling song is a sequence of about 6–10 echemes lasting about 3–5 s. The sequence begins very quietly, reaching maximum intensity after about 3–4 echemes. The echemes are separated by intervals of about 100–200 ms, often becoming more widely spaced towards the end of the sequence. Each echeme begins and ends very quietly, giving a spindle-shaped oscillogram (Fig. 118). Each of the later echemes in the sequence lasts about 300–400 ms and contains about 20–30 syllables repeated at the rate of about 80–90/s. The calling song is thus very similar to that of *llorenteae*, but is quieter and shorter, and has fewer echemes composed of fewer syllables.

DISTRIBUTION. North-eastern, central and south-eastern Spain.

Omocestus llorenteae Pascual

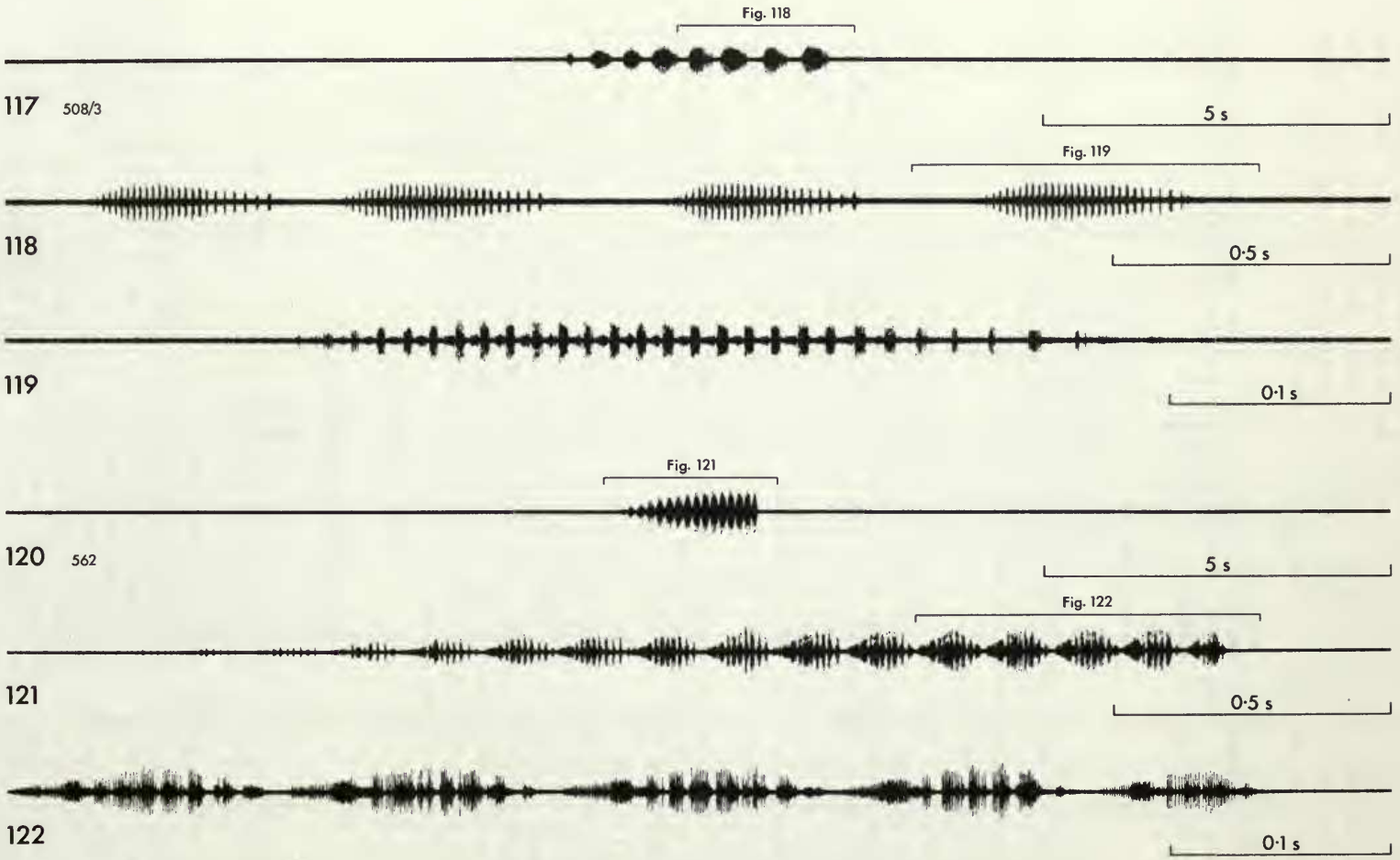
(Figs 123–128)

Omocestus llorenteae Pascual, 1978: 159. Holotype ♂, SPAIN: Granada, Sierra Nevada, Dornajo, 2000 m, 19.ix.1975 (*Pascual*) (Universidad de Granada) [examined].

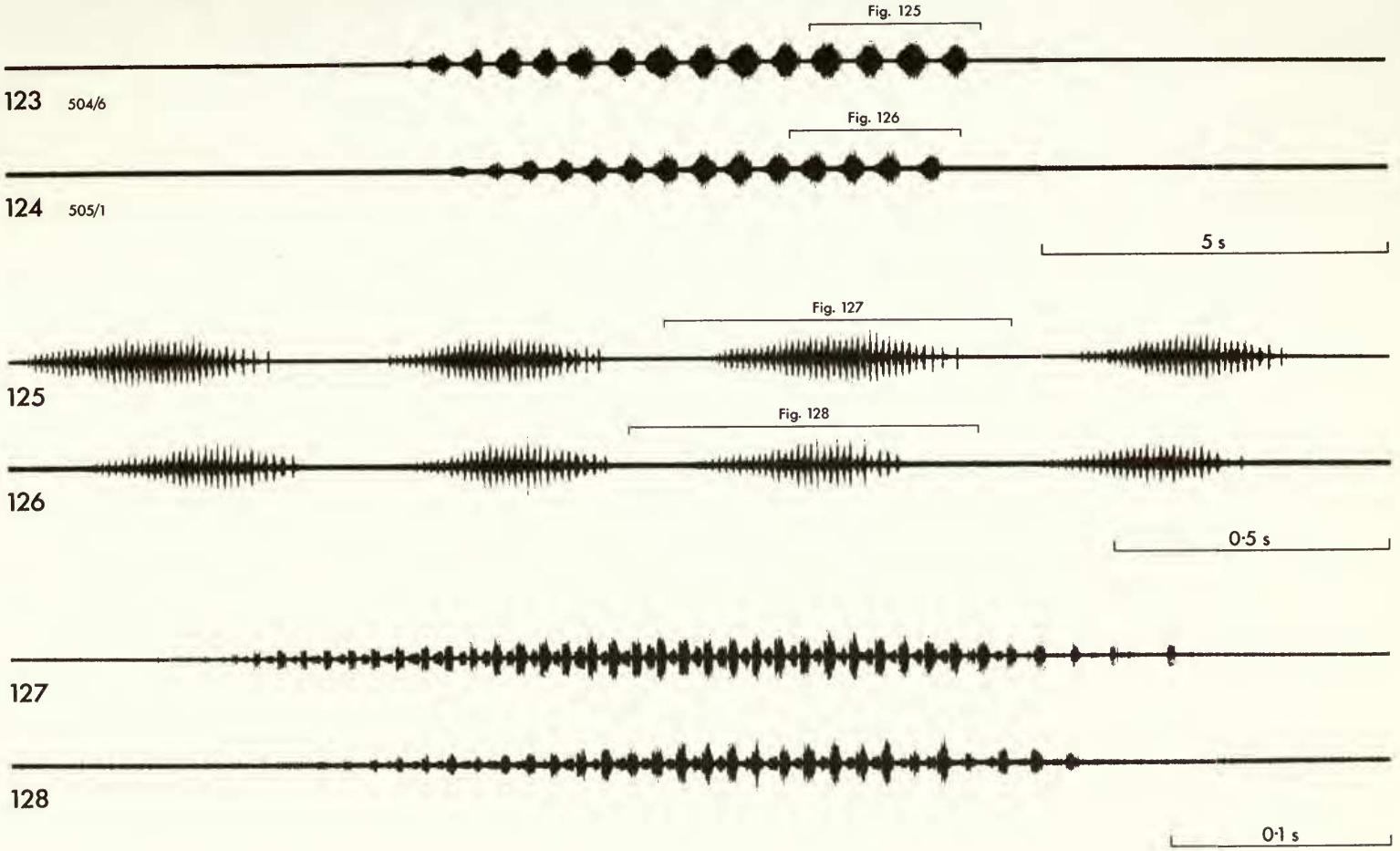
REFERENCES TO SONG. No published work known to me.

RECOGNITION. This species, known only from the Sierra Nevada and Sierra Espuña in southern Spain, can be distinguished from the similar montane species *uhagonii* and *bolivari* by the dark spots in the medial area of the fore wings and by the longer hind wings, which reach the tips of the fore wings; the longer hind wings also enable this species to be distinguished from *minutissimus*, which is in any case not known to occur in the Sierra Nevada or Sierra Espuña. Females of *llorenteae* also differ from those of *uhagonii* and *bolivari* in that the fore wings are more than twice the length of the pronotum.

In the field the calling song of the males, consisting of a rapid sequence of echemes, provides an easy means of distinguishing this species from most other species of *Omocestus* occurring in southern Spain.



Figs 117–122 Oscillograms at three different speeds of the male calling song of (117–119) *Omocestus minutissimus* and (120–122) *O. simonyi*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (p. 217).



Figs 123–128 Oscillograms at three different speeds of the calling songs of two males of *Omocestus llorenteae*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 217).

From *minutissimus*, which has a similar song-pattern, it may be distinguished by being longer (usually lasting more than 6 s) and having more echemes in each sequence (usually more than 11).

Song (Figs 123–128). The calling song is a sequence of about 11–15 echemes lasting about 6–8 s. The sequence begins quietly, reaching maximum intensity after about 5–6 echemes. The echemes are usually separated by intervals of about 100–200 ms, often becoming more widely spaced towards the end of the sequence. Each echeme begins and ends quietly, giving a spindle-shaped oscillogram (Figs 125, 126). By the middle of the sequence each echeme lasts about 350–600 ms and contains about 30–50 syllables repeated at the rate of about 85–95/s. The calling song is thus remarkably similar to that of *Myrmeleotettix maculatus* (Thunberg), though usually of shorter duration and composed of fewer echemes.

Distribution. Known only from the Sierra Nevada and Sierra Espuña in southern Spain.

Omocestus simonyi (Krauss)

(Figs 120–122)

Stenobothrus simonyi Krauss, 1892: 166. Syntypes of both sexes, Canary Islands: Lanzarote (*Simony*) (lost).

References to song. No published work known to me.

Recognition. This is the only species of *Omocestus* known from the Canary Islands and so in practice there is no problem in recognizing it. It is similar in appearance to *raymondi* but is smaller (total length less than 14 mm in the male, less than 19 mm in the female). The calling song of the male is superficially very similar to that of *uhagonii*, oscillographic analysis being required to show that it has far fewer gaps in each syllable; it differs from that of *raymondi* in having a much slower syllable repetition rate.

Song (Figs 120–122). The calling song is an echeme lasting about 1·0–2·5 s and consisting of about 10–20 syllables repeated at the rate of 5–10/s. Each echeme begins quietly, reaching maximum intensity about midway through its duration. Oscillographic analysis shows that there are gaps in each syllable, similar in number to those in the calling song of *raymondi* (far fewer than in *uhagonii*) but not arranged in the same pattern and maintained until the end of the echeme (Figs 121, 122). The echemes are repeated at irregular intervals.

Distribution. Known only from the Canary Islands, where it occurs on Lanzarote and Fuerteventura.

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